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PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON

169th Session (1956–57)

Vol. 169 Parts 1 and 2

CONTENTS

Page

Proceedings, 4 *October* 1956 to 24 *May* 1957, including papers printed in abstract 1

Anniversary Meeting, Reports and Accounts, etc 14

Presidential Address 134

Additions and Gifts to the Library, and Benefactions 27

Obituaries 35

Papers printed in full:—

Joint Discussion with the Systematics Association on "The Inheritance of Acquired Characters"

Opening Address. By H. Graham Cannon 41

Automatic Adjustments in Bacterial Populations in Response to Environmental Changes. By A. C. R. Dean 45

Possible Mechanisms for the Inheritance of Acquired Characters. By R. Melville 49

Inheritance of Acquired Characters. By C. H. Waddington 54

General Discussion 61

Inhibition of Germination of the White Mustard by Bryony Juice. By I. Henry Burkill 62

The Fisheries Laboratory, Lowestoft.

An effect of Low Temperature on the Osmo-Regulatory ability of the Cod (*Gadus callarias*) in Arctic Waters. By P. M. J. and A. D. Woodhead 63

Marine Fish Larvae and the Osmotic Hazard. By J. E. Shelbourne 65

Symposium on Aerobiology.

The Automatic Volumetric Spore Trap and Examples of its Use in Plant Pathology. By J. M. Hirst 66

The Incidence of Atmospheric Pollen and Spores in Great Britain considered from the point of view of Allergy. By H. A. Hyde ... 66

Aphid Dispersal and Diurnal Periodicity. By L. R. Taylor 67

Atmospheric Movements and the Biology of the Desert Locust (*Schistocerca gregaria*). By R. C. Rainey 73

Some Aspects of Floral Vascular Systems. By K. R. Sporne 75

[*Continued over*

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1958

CONTENTS—*contd.*

SYMPOSIUM ON PLANT-PARASITIC NEMATODA.

Introduction. By B. G. PETERS 84

Potatoes Resistant to Root Eelworm. By T. D. WILLIAMS 93

On a Disease Complex of Strawberries involving a Nematode and a Bacterium. By R. S. PITCHER and J. E. CROSSE 105

SYMPOSIUM ON WEED KILLERS.

Weed Control in Crops. By R. L. WAIN 105

Wild Oats. By J. STUBBS 106

The Use of Selective Weedkillers in the Control of Vegetation on Roadside Verges. By OLIVE BALME 107

The Potential Value of Herbicides in Nature Reserves. By J. D. FRYER 107

SYMPOSIUM ON CYTO-TAXONOMY.

Introduction. By W. B. TURRILL 110

Problems in Mammalian Cytotaxonomy. By J. L. HAMERTON 112

Chromosomes and Taxonomic Importance. By A. J. CAIN 125

Effects of Outcrossing on the Chromosome Number in Vertebrates. By M. FISCHBERG 129

A Cytological Comparison of Nearctic and Palaearctic representatives of *Chironomus tentans* (Diptera). By A. B. ACTON 129

Chromosomes and Fern Phylogeny. By IRENE MANTON 132

The Cytotaxonomy of a Tropical Fern Complex. By T. G. WALKER 132

Cytotaxonomy of the Rostrate Violets. By D. H. VALENTINE 132

PRESIDENTIAL ADDRESS. Palaebotany and the Evolution of the Flowering Plants. By H. HAMSHAW THOMAS 134

The Dick Herbarium: additional note. By Sir GAVIN DE BEER 143

Logic and Memory in Linnaeus's System of Taxonomy. By A. J. CAIN 144

Genetic Stability in the Snail *Cepaea nemoralis*: a further example. By C. B. GOODHART 163

NOTE

Index, Title-page and Contents of Vols. 163 to 168 in preparation.

PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON
Session 1956–57

Vol. 169 Parts 1 and 2

PROCEEDINGS OF THE GENERAL MEETING HELD ON 4 October 1956

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the Anniversary Meeting held on 24 May 1956, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. H. A. Hyde, Dr. Max Pettersson, the Executors of the late Mr. F. J. F. Barrington, the Carlsberg Foundation, Messrs. Faber & Faber, publishers, the City Parochial Foundation, Dr. N. Ahmat, the Board of Research Studies, Cambridge, the University of Washington Library, Messrs. Thames & Hudson, publishers, Messrs. McGraw-Hill, publishers, Messrs. Bell & Sons, publishers, The Pilgrim Trust, Professor P. Brien, Miss E. Armitage, Mr. Denys Morgan, the Nature Conservancy, Mr. A. L. Galliford, Professor R. E. Holttum, Dr. H. Züllig, the Freshwater Biological Association, Lady Charlotte Bonham-Carter, Dr. B. O. Landin, Rev. H. Santapau, S. J., Sir Frederick Stern, O.B.E., M.C., Dr. K. V. O. Dahlgren, Director of Agriculture, Nyasaland, Dr. P. H. A. Sneath, Hope Department of Entomology, Oxford, Mr. S. A. Manning, National Botanic Gardens, Lucknow, the Sudan Embassy in London, the International Commission on Zoological Nomenclature and Dr. L. Chalk.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Dr. Charles Edmond Bradlaugh Bonner, Mrs. Anna Nellie Griffith, M.A., Mr. Malcolm Cyril Jacobs, B.Sc., Mr. John Lewis, B.Sc., Dr. Kenneth Robert Sporne, Mr. Frank White, M.A., Mr. John Nevison Wilson, B.A., Mr. Geoffrey Honorth Spencer Wood, M.A. and Dr. Elwood Curtin Zimmerman.

The President reported the death of Cecil Prescott Hurst, John Withers Lester, Arthur Mayfield, William Marshall and Prof. Doris Livingston Mackinnon, Fellows.

The President announced that Mr. Warton's Testimonial Fund would soon be closed and requested that any further contributions should be forwarded as soon as possible.

The following comminication was read and discussed :—

Dr. Bassett Maguire (Visitor). Return to the collecting grounds of Richard Spruce. Present Day Exploration in the Headwaters of the Río Orinoco, Casiquiare and Rio Negro, South America. Illustrated with a 16 mm. Kodochrome film. (Discussed by Mr. E. J. H. Corner, F.R.S., Mr. N. Y. Sandwith and Mr. P. R. Bell ; Dr. Maguire replied.)

Abstract—

Since 1944, the speaker has been actively engaged in botanical exploration in the Guayana Highland of southern Venezuela and contiguous British Guiana, Brazil and Colombia for The New York Botanical Garden.

The Guayana Highland is an ancient and remote region of isolated lofty sandstone tabular mountains which first became known to the scientific world through the explorations of Robert and Richard Schomburgk; chiefly from the former's momentous journey in 1838 after his " discovery " of Mt. Roraima, westerly across all of Guayana to the Orinoco River. At the beginning of the nineteenth century, Humboldt and Bonpland collected plants and made astronomical observations at Esmeralda at the base of Cerro Duida, at the headwaters of the Orinoco. A little more than a half century later, Richard Spruce, the supreme collector of tropical American plants visited the same Esmeralda savannas.

Through the turn of the nineteenth century, exploration continued at the two extremes of the east–west axis of the Highland. Chiefly in the east the visits of im Thurn, McConnell and Quelch, Ule and others at Roraima, on the tri-corners of British Guiana, Venezuela and Brazil, lent evidence that Roraima was the seat of a remarkable plant endemism. (" The Lost World " of Conan Doyle is to be associated with Roraima.) At the western end, the explorations of Cerro Duida by G. H. H. Tate added conclusive proof that the Roraima sediments of all the Guayana Highland supported a flora of outstandingly high endemism and phytogeographic and phyletic significance.

Influenced by these considerations, The New York Botanical Garden has over the past twelve years completed sixteen expeditions, conducted largely by the speaker, to some twenty-five table mountains of Guayana. The accompanying film records the first exploration of Cerro Yutaje in the upper Orinoco drainage, a visit with the primitive forest Amerindian, the Guaikas, and the " discovery " and ascent of Cerro de la Neblina along the Venezuelan-Brazilian frontier.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 18 October 1956

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 4 October 1956, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. M. W. Holdgate, Mr. D. Morgan, Messrs. Nicholas Kaye, Ltd., publishers, Messrs. Bailey Bros. & Swinfen, Ltd., publishers, Prof. A. C. Hardy, F.R.S., Dr. Gunnar Lundberg, Mrs. W. H. Walton and Mr. W. W. A. Phillips.

Dr. Charles Burford Goodhart signed the Obligation in the Roll and Charter Book and was admitted a Fellow.

Certificates of recommendation for election to Fellowship were read for the first time in favour of the following :—Peter Adames, M.A., James Percy Tufnell Burchell, M.C., William Peter Crowcroft, M.Sc., D.Phil., John Kevin Patrick Kennedy-O'Byrne, Donald Joseph Boomer Killick, M.Sc., Miss Esther Judith Grant Kirkwood, B.Sc., Julian Rzóska, D.Phil., James Robert Tennant, B.Sc., and Trevor Angus Villiers, B.Sc.

The following communications were read and discussed :—

Mr. Harry V. Thompson (Visitor). Myxomatosis and the Rabbit in Britain. (Discussed by Dr. Hugh Scott, Mr. E. Milne-Redhead, Mr. W. E. Hollows, Dr. E. B. Worthington, Dr. Edward Hindle, Mr. R. J. A. W. Lever and Dr. R. Melville; Mr. Thompson replied.)

Abstract—

Reference was made to the following:—

1. The position of the rabbit in Britain before Myxomatosis. 2. The arrival of the disease in 1953, and its subsequent spread. 3. The direct and indirect effects of very widespread rabbit reduction and 4. The future of the rabbit and the disease.

Mr. H. R. Hewer, Sec. L.S. The Method of dispersal of animals. (Discussed by Dr. E. B. Worthington, Mrs. E. Milne-Redhead, Mr. W. E. Hollows, Dr. C. B. Goodhart, Mr. H. V. Thompson, Dr. E. H. Eason, Dr. Edward Hindle, Dr. B. P. Uvarov, Dr. R. C. Rainey, and Dr. R. Melville ; Mr. Hewer replied.)

Abstract—

Most geographical work on animals is concerned with static distribution. Little is known of the detailed way in which animals increase or decrease the area occupied by the species. Some general considerations were put forward as a possible line of investigation.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 1 November 1956

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 18 October 1956, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. A. V. Bogdan, Dr. E. Marcus, King's College, London, Dr. A. Tindall Hopwood and Mr. A. A. Bullock.

Mr. Peter Raymond Slater Hunt, The Rev. Réné Lovocat and Mr. Donald Leatherdale signed the Obligation in the Roll and Charter Book and were admitted Fellows.

The President reported the death of Mr. Henry Nicholas Ridley, C.M.G., F.R.S., F.L.S., and moved the following Resolution, which was passed in silence, all present standing in their places :—

> The Fellows of The Linnean Society of London, having heard with the very deepest sorrow of the death of Henry Nicholas Ridley, C.M.G., F.R.S., desire to place on record their high appreciation of his services rendered to the science of Natural History and to the Society during his seventy-four years of Fellowship. Elected in 1881 he served on the Council from 1888–89, 1912–13 and 1914–15 and was appointed a Vice-President 1914–15. In 1950 he was awarded the Society's highest honour, the Linnean Gold Medal. At the age of 100 he was the oldest member of the Society and throughout his long Fellowship he showed the greatest interest in the activities of the Society
>
> Deploring the loss of so distinguished a Fellow, the Fellows desire to express to Mrs. Ridley their deepest sympathy in her bereavement.

Certificates of recommendation for election to ordinary Associateship were read for the first time in favour of Miss Lesley Elliott-Fletcher, John F. Peake and Alan Louis Geoffrey Sapper, and certificates of recommendation for election to Fellowship were read for the second time in favour of those candidates whose names appear in the Minutes of the Meeting held on 18 October 1956.

JOINT DISCUSSION WITH THE SYSTEMATICS ASSOCIATION

A joint discussion with the Systematics Association : " The Inheritance of Acquired Characters ", was opened by Prof. H. Graham Cannon, F.R.S., Dr. A. C. R. Dean, Dr. R. Melville, and a contribution by Prof. C. H. Waddington, F.R.S. was read in his absence by Dr. A. J. Cain.

A general discussion followed, in which the following took part :—the President, Dr. W. B. Turrill, O.B.E., Dr. Max Pettersson, Mr. P. F. Mattingly, Dr. A. J. Cain, Dr. S. M. Manton, F.R.S., Mrs. J. Kennedy, the Rev. Réné Lovocat and Mr. R. Ross. Prof. Graham Cannon, Dr. Dean and Dr. Melville replied. **[Papers printed on p. 41.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 15 November 1956

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 1 November 1956, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—The Director, Royal Botanic Gardens, Kew, Dr. Hugh Scott, F.R.S., the University of Birmingham, the Trustees of the British Museum and Mr. R. H. Jeffers.

The following candidates for Fellowship and Ordinary Associateship were ballotted for and elected :—Fellows :—Peter Adames, M.A., James Percy Tufnell Burchell, M.C., William Peter Crowcroft, M.Sc., D.Phil., John Kevin Patrick Kennedy-O'Byrne, Donald Joseph Boomer Killick, M.Sc., Miss Esther Judith Grant Kirkwood, B.Sc., Julian Rzóska, D.Phil., James Robert Tennant, B.Sc. and Trevor Angus Villiers, B.Sc. Ordinary Associates :—Miss Lesley Elliott-Fletcher, John F. Peake and Alan Louis Geoffrey Sapper.

The following communications were read and discussed :—

Mr. I. Henry Burkill, F.L.S. (Exhibit). The inhibition of germination of the White Mustard (*Brassica alba* Boiss.) by contact with juice from the berries of the Common Black Bryony (*Tamus communis* L.). (Discussed by Dr. C. R. Metcalfe, Dr. R. Melville and the President.) **[Paper printed on p. 62.]**

THE FISHERIES LABORATORY, LOWESTOFT

Mr. J. E. Shelbourne. Marine fish larvae and the Osmotic hazard. **[Paper printed on p. 65.]**

Mr. P. M. J. and Mrs. A. D. Woodhead. An effect of low temperatures on the osmo-regulatory ability of cod (*Gadus callarias*) in Arctic waters. (Discussed by Dr. J. P. Harding, Dr. Margaret E. Brown, the President, Dr. R. Melville and Dr. R. McConnell ; Mr. and Mrs. Woodhead replied.) **[Papers printed on p. 63.]**

PRESIDENT'S RECEPTION
6 December 1956

The PRESIDENT, Dr. H. Hamshaw Thomas, M.B.E., F.R.S., received the Guests in the Library.

A coloured film, "Ron Mor on Shillay" (The Grey Seal in the Hebrides), with a commentary by Mr. H. R. Hewer, Sec. L.S., was shown in the Meeting Room.

EXHIBITS IN THE LIBRARY AND COUNCIL ROOM.

The Council was greatly indebted to the DIRECTOR OF THE ROYAL BOTANIC GARDENS, KEW, for providing the decorative plants exhibited throughout the Library.

The Council was also indebted to Mr. F. O. MOSELEY, F.L.S., for the cut flowers displayed.

Professor TOM M. HARRIS, F.R.S., F.L.S. A burnt Mesozoic flora from limestone fissures in Glamorgan.

BRITISH MUSEUM (NATURAL HISTORY), DEPARTMENT OF ZOOLOGY. X-ray Microscopy as an aid to the study of Foraminifera. (Shown by Mr. R. H. Hedley.)

The tests of Foraminifera, with their great variety of internal structures, would appear to be suitable objects for a radiographic technique. The present practice of sectioning a test in order to determine the internal structure is time-consuming and the specimen is inevitably destroyed. Other methods of demonstrating test morphology such as dissection techniques, with or without the aid of impregnating or support substances, also involve the destruction of the specimen.

The method employed in the production of the photographs demonstrated is one known as "contact microradiography". This involves the production of an X-ray image, or radiograph by "soft" X-rays (X-rays of relatively long wave length). This X-radiation is directed on to a photographic emulsion on which is placed the object for study. The resultant X-ray image may then be examined with an optical microscope or from it a photomicrograph can be obtained.

Because of the small size of the Foraminifera they must be first mounted on a suitable surface rather than being placed immediately next to the photographic emulsion. This was done by mounting them with the aid of gum tragacanth on a "Styrafoil" (12.5 μ thick) sheet, which is held tight by cellulose tape within the frame of a cardboard holder. This unit is then placed firmly on to the Kodak Maximum Resolution Plate, the almost grainless emulsion of which is essential in the production of good microradiographs of small Foraminifera.

ROYAL BOTANIC GRADENS, KEW. Some Ferns and Fern Allies cultivated at Kew.

QUEEN MARY COLLEGE, BOTANY DEPARTMENT. Chromosomes of the Euglenineae. (Shown by Mr. Gordon Leedale.)

Mr. RICHARD HAMOND. Drawings of Marine Animals mainly from Norfolk and the West of Ireland.

Mr. D. N. PATON, F.L.S., A.R.P.S. Coloured transparencies of the flora of Tenerife.

During April 1956 the author visited the island of Tenerife, when he was able to obtain a number of colour photographs of the flora there. Among them are many endemics, in identifying of which he is most grateful for the help received there from Dr. Eric Sventenius, Director of Jardin de Aclimatacion de la Orotava.

British Museum (Natural History). Department of Botany Endemism in Jamaica as illustrated by the Genus *Columnea*. (Shown by Mr. W. T. Stearn, F.L.S.)

The Fisheries Laboratory, Lowestoft. The Osmotic Hazard.

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., Pres.L.S.

(*a*) Autograph letters of famous botanists.
(*b*) A testimonial for Daniel Oliver written by J. D. Hooker and also signed by his father W. J. Hooker.

Mr. A. A. Bullock, F.L.S. A sidelight on travel in Central Africa.

In remote regions roads are usually no more than mud tracks, and bridges rarely survive the rainy season. A series of photographs illustrated the construction of a " drift " over the Mambwezi River after the bridge near Nsama had been washed away but before the river was fordable by a heavy vehicle.

The Mambwezi River flows into the seasonal swamp grasslands of one of the Red Locust outbreak centres—the Mweru wa Ntipa and its very shallow salt lake near the Congo border in north-eastern Northern Rhodesia.

The Royal Horticultural Society. Drawings of Plants made in China by Chinese Artists for the Society between 1812 and 1831.

The Zoological Society of London. Some interesting Animals from the Society's Collection (Mammals, Birds and Reptiles).

1. A specimen of the Moon Rat (*Echinosorex gymnura*); not a rodent but a very primitive insectivore.

2. A number of interesting birds which had recently been received including the following:

Great Green Cacique (*Ostinops viridis*).
Yellow-billed Oxpecker (*Buphagus africanus*).
Black-throated Cardinal (*Coccopsis gularis*).
Yellow-crowned Troupial (*Icterus chrysocephalus*).
Queen of Bavaria's Conure (*Aratinga guarouba*).
Red-throated Parrot (*Amazona collaria*).

The Oxpeckers are noted for their habit of perching on the backs of large game animals and removing the ticks which infest them.

3. A collection of lizards from various parts of the world included the following:

Calotes jubatus from South-east Asia.
Hemitheconyx caudicinctus from West Africa.
Brookesia platiceps from East Africa.
Amphibolurus barbatus from Australia.
Varanus salvator from South-east Asia.
Anolis carolinensis from South-eastern U.S.A.
Tupinambis teguexin from South America.
Pholidobulus montium from the Andes of Ecuador.

Mr. E. M. MARSDEN-JONES, F.L.S. and Dr. W. B. TURRILL, O.B.E., F.L.S. Variation in leaf shape in the bladder campions (*Silene* spp.)

Investigations by various methods on the taxonomy, genetics and ecology of the bladder campions have been carried out at Kew and Potterne (Wilts) for the past thirty years. The results have been prepared for publication in book form. In the present exhibit a very small selection of samples illustrates the wide range of variation in leaf shape in the group and a few of the genetical and other results obtained in experimental and field researches. Leaf shape was chosen for exhibition from amongst many other characters investigated because it is easier to demonstrate by specimens and photographs than other characters.

EAST MALLING RESEARCH STATION. Spring Frost Damage to Apples.

Mr. H. I. MATTHEWS, O.B.E., M.C., F.L.S., Imperial College, London. Electron-micrographs of Chalk and Deep-sea Deposits.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 17 January 1957

Dr. H. HAMSHAW THOMAS, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 15 November 1956, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. E. L. Little, Dr. H. Dodge, Department of Zoology, University of Queensland, Messrs. Longmans, Green & Co. Ltd., publishers, Mr. R. S. George, Mrs. M. L. Sprague, Mr. A. E. Haarer, the Nature Conservancy, Mr. A. L. Galliford, Prof. M. Locquin, Dr. R. S. Palmer, Director of Agriculture, Sierra Leone. Dr. E. E. Sherff, Prof. R. C. McLean, Secretary of National Institute of Oceanography, Secretary of Royal College of Surgeons of England, Director of National Museum of Wales, Dr. Hugh Scott, F.R.S., Mr. H. L. G. Stroyan, Prof. K. Tsuneki, and Mr. R. H. Hudson.

Dr. William Peter Crowcroft and Mrs. Margaret Steentoft Nielsen, signed the Obligation in the Roll and Charter Book, and were admitted Fellows.

The PRESIDENT reported that in order to conserve shelving space and reduce the cost of binding, certain proposals were being made to dispose of some sets of periodicals of a general nature and readily available elsewhere in London, and for the retention of others for only a limited period.

Full particulars of these proposals would remain suspended in the Library for the perusal of Fellows until the Anniversary Meeting.

The PRESIDENT reported that a Congratulatory Message on behalf of the Fellows had been sent to Mr. William Stone, M.A., a Fellow for 78 years, on his One-Hundredth Birthday on 14 January 1957.

The PRESIDENT announced that in commemoration of the 250th Anniversary of the birth of Linnaeus, a Reception would be held on the Evening of Thursday, 30 May 1957.

The PRESIDENT also announced that the General Meeting, arranged for Thursday, 2 May, would now be held on Friday. 3 May 1957, and that as an experiment there would be an additional General Meeting on 18 July 1957 to enable overseas Fellows and visitors to attend a General Meeting of the Society.

In presenting Mr. W. S. Warton with a cheque for £112, being the contri-

butions received from Fellows to the Librarian's Testimonial Fund the PRESIDENT said :

Mr. W. S. Warton, it was with sincere regret that the Officers, Council and Fellows of this Society learned that the time had come when you felt it necessary to relinquish your work for the Society which you had performed so zealously and efficiently for no less than 40 years.

You came to us in 1916 as Assistant Librarian but very soon afterwards you found yourself faced with the greater part of the work in the Library, and you have carried a major part of the burden ever since. I know that this was very considerable, especially from 1928 to 1954, when the Society's library was associated with the scheme for a National Central Library for Students and such a large number of books had to be sent out. You were appointed Librarian in 1951.

Our library has been heavily handicapped for lack of funds, and for this reason the Society should remember with gratitude the devoted work which you and others have done under discouraging conditions. As a Fellow for more than 30 years I know how ready you have always been to try to help us to find the books we wanted, and to post them to us when we were away from London. Many of us find it difficult to envisage the Library without you.

To-day I have the pleasure of handing to you a cheque for £112 on behalf of the Fellows of the Linnean Society as a token of their regard and appreciation. With it I wish to convey to you the sincere thanks of the Society for your invaluable work. May I express the hope that in retirement your health will improve and that you have many happy years before you.

Mr. Warton expressed his grateful thanks for the gift.

The following communications were read and discussed :—

Sir FREDERICK STERN, O.B.E., M.C. Flowering Plants of Cape Province, illustrated by coloured transparencies. (Discussed by the President, Dr. T. T. Barnard, and Prof. R. S. Adamson ; Sir Frederick Stern replied.)

Mr. E. MILNE-REDHEAD. Some glimpses of Southern Tanganyika, illustrated by coloured transparencies. (Discussed by the President, Mr. A. E. Harrer, Dr. W. B. Turrill, Mr. J. B. Gillett, Dr. John Ramsbottom, Mr. E. J. H. Corner and Dr. D. Rhind ; Mr. Milne-Redhead replied.)

Abstract—

The Southern Province of Tanganyika has been, until recently, comparatively poorly known botanically. This applies especially to the Songea District, which is situated in the corner between Lake Nyasa and Mozambique. This district was visited by the German collector, W. Busse, in 1901, but many of his specimens were destroyed in Berlin. Similarly a considerable proportion of the collection made by the Austrian collector, H. Zerny in 1935–36 was destroyed at Vienna, but some specimens collected at about the same time by F. Zimmer are in the British Museum (Natural History). The present expedition from Kew, made possible by the financial help of the Colonial Office and consisting of Mr. E. Milne-Redhead and his colleague, Mr. P. Taylor, F.L.S., concentrated on collecting in the Songea District throughout the rainy season of 1955–56. The photographs showed mainly scenery and vegetation and conveyed a good impression of this little-known part of Tanganyika. The coloured transparencies were all taken by Mr. Taylor.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 7 February 1957

Asst. Professor H. R. Hewer, Zoological Secretary, in the Chair.

The Proceedings of the General Meeting held on 17 January 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. A. E. Haarer, Mrs. E. A. Hodgson, Mr. R. N. Lyne, Director, National Botanical Gardens, Lucknow, Mrs. M. Pallis, Prof. J. W. Heslop-Harrison, F.R.S., Dr. N. Ahmad, Mr. Philip A. R. Street and Director, Transvaal Museum.

Miss Esther Judith Grant Kirkwood, B.Sc., and Mr. James Robert Tennant, B.Sc., signed the Obligation in the Roll and Charter Book, and were admitted Fellows.

Reported the deaths of Henry James Howard and Sir William Wright Smith, Kt. F.R.S., Fellows.

The following Alteration to Bye-Law, Chap. 13, Sec. 1., proposed by the Council to facilitate the holding of some General Meetings of the Society on days other than Thursdays, was read for the first time, viz.:—

> "The General or Ordinary Meetings of the Society shall be held on such Thursdays or other days as the Council may decide. Due notice of the days, hours and place of Meetings shall be given to every Fellow whose address is known."

The following communications were read and discussed :—

Dr. Victor B. Scheffer (Visitor). The Fur-seal Islands of Alaska.

Abstract—

The Author traced the history of the northern fur-seals (*Callorhinus ursinus*) from their discovery by Russians in 1786, through various stages of commercial exploitation to the present day. The Pribilof population has increased over ten-fold since its threatened extermination in 1911. At a treaty convention in Washington in the fall of 1955, attended by delegates from Canada, Japan, the United States and the USSR, a new look was taken at proposals to achieve the "maximum, sustainable economic productivity" of the seals for the benefit of the North Pacific Nations.

Coloured transparencies of the Pribilof Islands, photographed by the Author on ten trips, were shown. Emphasis was placed on biological studies of the fur-seals as a basis for wise and continued conservation.

Professor R. Vaz Ferreira (Visitor). The Seal Islands of Uruguay.

Abstract—

The seal islands of Uruguay, situated between 33° 56′ and 35° 01′ south latitude, are inhabited by important herds of *Otaria byronia* and *Arctocephalus australis*, both of which reach there the northern limit of their successful breeding grounds on the Atlantic side.

The biological research about these herds, whose exploitation by white man started at the beginning of the sixteenth century, has only recently been initiated.

In the communication, the author described the social structure of both species and the outstanding characters of their behaviour, pointing out the

survival value in that zone of certain patterns of behaviour, such as selection of definite soil topography for breeding, pup bathing etc.

Coloured slides taken by the author were shown.

(These papers were discussed by Dr. F. C. Fraser, Mr. E. N. Nicholson, Dr. E. B. Worthington, Zoological Secretary, Mr. R. J. G. Savage, Dr. R. M. Laws and Dr. I. Gordon ; Dr. Scheffer and Prof. Vaz Ferreira replied.)

PROCEEDINGS OF THE GENERAL MEETING HELD ON 21 February 1957

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 7 February 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. A. E. Haarer, Prof. G. C. Varley, the Librarian, Universitets-biblioteket, Uppsala, and Mr. A. C. Townsend.

Donald Joseph Boomer Killick, M.Sc., signed the Obligation in the Roll and Charter Book, and was admitted a Fellow.

The President announced that the Council had nominated Dr. M. A. Pocock, F.L.S., for the Crisp Award and Medal and that Dr. W. B. Turrill, O.B.E., F.L.S., had been invited to deliver a Hooker Lecture during the next Session.

The proposed Alteration to Bye-Law, Chapter 13, Sect. 1, was read for the Second time.

SYMPOSIUM ON AEROBIOLOGY

A Symposium on Aerobiology was opened by Dr. J. M. Hirst, " The automatic volumetric spore trap and examples of its use in plant pathology " ; Mr. H. A. Hyde, " The incidence of atmospheric pollen spores in Great Britain, considered from the point of view of allergy " ; Mr. L. R. Taylor, " The origin and dispersal significance of fluctuations in aerial aphid density " and Dr. R. C. Rainey, " Atmospheric movements and the biology of the Desert Locust ".

In a general discussion the following also took part :—Mr. P. K. C. Austwick, Dr. John Ramsbottom, Mr. D. Etherington, the Zoological Secretary, Dr. R. Melville, Mr. H. F. van Emden, Mr. T. Lewis, Mr. J. G. Skellam and Dr. L. Ogilvie. **[Papers printed on p. 66].**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 7 March 1957

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 21 February 1957 having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Forest Research Institute, Dehra Dun, Field Studies Council, Dr. H. Zullig, Mr. S. S. Ghosh, Dr. N. Ahmad and Mr. A. W. Greene.

Sidney John Relph, B.Pharm. signed the Obligation in the Roll and Charter Book, and was admitted a Fellow.

The alteration to Bye-law, Chapter 13, Sec. 1, proposed by the Council to facilitate the holding of some General Meetings of the Society on days other than Thursdays, was Balloted for and approved, viz.:—

> " The General or Ordinary Meetings of the Society shall be held on such Thursdays or other days as the Council may decide. Due notice of the days, hours and place of Meetings shall be given to every Fellow whose address is known."

Certificates of Recommendation for Election to Fellowship in favour of the following were read for the first time :—Pramatha Kanta Chowdhuri, M.Sc., Ph.D., Dunkery Hugh Dalby, B.Sc., Ph.D., Mrs. Dorothy Fernando, David John Hambler, Ph.D., Sydney Gerald Harrison, B.Sc., Donald Gordon Ineson, LL.D., D. J. Lewis, M.A., Sc.D., Edward Stewart Maurer, Frederick Michael Percival Maurice, V. Raghavan, M.Sc., Seshagiri Rao Rolla, M.Sc., The Lord Strathcona and Mount Royal, Thomas Douglas Victor Swinscow, M.R.C.S. Eng.), L.R.C.P. (London), M.B., B.S., Mrs. Edith Gertrude Thomas, M.A.

The PRESIDENT reminded Fellows that proposals for Officers and New Members of Council under Bye-Law, Chap. 8, Sec. 2 and recommendations for Foreign Members and Associates *honoris causa*, should be forwarded to the General Secretary not later than 5 April 1957.

The following communications were read and discussed :—

Dr. K. R. SPORNE. Some aspects of floral vascular systems. (Discussed by the President, Dr. R. E. Holttum, Mr. E. J. H. Corner, Dr. W. B. Turrill and Mr. F. Rose ; Dr. Sporne replied.) **[Paper printed on p. 75.]**

Dr. R. MELVILLE. The nature of the Angiosperm ovary and the origin of The Angiosperms. (Discussed by Dr. W. B. Turrill, Dr. Marie Stopes, Dr. K. R. Sporne, the President and Dr. K. L. Alvin : Dr. Melville replied.)

Abstract—

A number of features of the vascular systems of Angiosperm ovaries are not consistent with any variation of the carpel theory. This, coupled with the absence of fossils with the structure required by the carpel theory for a " pro-angiosperm ", suggests that this theory is based on false premises. An examination of the vascular structure of the ovaries of representatives of a number of Angiosperm families has revealed that an alternative mode of origin is probable. A new theory of the origin of the Angiosperms was put forward, which was supported by numerous fossils having the structure required for the appropriate " pro-angiosperm ". So-called " solid " and " semi-solid " carpels find a simple explanation in the new theory, which also accounts for the origin of the stigma and the various types of placentation.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 21 March 1957

Dr. H. HAMSHAW THOMAS, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 7 March 1957 having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting : Mr. R. Ross and Professor F. W. Jane.

John Kevin Patrick Kennedy-O'Byrne signed the Obligation in the Roll and Charter Book, and was admitted a Fellow.

The PRESIDENT reported the following deaths :—His Honour Judge H. Drysdale Woodcock, Q.C., Fellow, and Benjamin Storrow, M.Sc., Associate *honoris causa*.

Certificates of Recommendation for Election to Fellowship were read for the second time in favour of those candidates whose names appeared in the Minutes of the Meeting held on 7 March 1957.

SYMPOSIUM ON PLANT PARASITIC NEMOTODA

A Symposium on Plant-Parasitic Nematoda was opened with an introduction by Professor P. G. Peters ; Mr. N. G. Hague, " Population studies on cyst-forming nematodes " ; Mr. T. D. Williams, " Potatoes resistant to root eelworm " and Dr. R. S. Pitcher " On a disease complex of strawberries involving nematoda and a bacterium ".

In a general discussion the following also took part :—Mr. D. Leatherdale, Mr. J. J. Hesling, Mr. P. R. S. Hunt, Dr. F. R. Tubbs, and Dr. J. E. Crosse. **[Papers printed on p. 84.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 18 April 1957

Dr. H. HAMSHAW THOMAS, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on 21 March 1957 having been circulated, were taken as read, and confirmed.

The PRESIDENT reported that on the afternoon of Wednesday, 17 April 1957, the Society had been honoured by a visit from His Majesty The King of Sweden, who, accompanied by His Excellency the Swedish Ambassador and Lt.-Col. Jan C. von Horn, A.D.C., to His Majesty, had spent nearly one hour looking at a selection from Linnaeus's Collections, Books and Manuscripts.

The President later announced, that during the General Meeting interval Lt.-Col. Jan C. von Horn, on behalf of His Majesty, had presented the Society with a cheque for £100 for expenditure on the Society's Library.

These announcements were received with acclamation and a Resolution was unanimously approved expressing the Society's most grateful thanks to His Majesty for his great interest in the Society and for his generous gift.

The following were thanked for gifts made to the Library since the last Meeting :—Professor R. Ruggles Gates, F.R.S., Mr. H. R. Marshall, Professor R. S. Adamson, Messrs. G. Bell & Sons, publishers, Professor Dr. K. Berg and Professor Roger Heim, F.M.L.S.

Robert Stephen George, Dennis Roy Green, B.Sc., Clifford Mortlock, M.Sc., and David Philcox signed the Obligation in the Roll and Charter Book and were admitted Fellows.

Certificates of Recommendation for Election to Fellowship were read for the first time in favour of K. C. Basu Chaudhary, M.Sc., Robert Gordon Darlington, Jagannath Dattatraya Kulkarni, B.Sc., B.Pharm., Ph.D., Samuel Frank Loring, M.A., Frederick Richard McQuown, M.A. and Donal Walker, B.Sc., M.A., Ph.D.

The following candidates for Fellowship were balloted for and elected :—Pramatha Kanta Chowdhuri, M.Sc., Ph.D., Dunkery Hugh Dalby, B.Sc., Ph.D., Mrs. Dorothy Fernando, David John Hambler, Ph.D., Sydney Gerald Harrison, B.Sc., Donald Gordon Ineson, LL.D., D. J. Lewis, M.A., Sc.D., Edward Stewart Maurer, Frederick Michael Percival Maurice, V. Raghavan, M.Sc., Seshagiri Rao Rolla, M.Sc., The Lord Strathcona and Mount Royal,

Thomas Douglas Victor Swinscow, M.R.C.S. (Eng), L.R.C.P. (London), M.B., B.S., and Mrs. Edith Gertrude Thomas, M.A.

SYMPOSIUM ON WEED KILLERS

A Symposium on Weedkillers was opened by Professor R. L. Wain (Visitor), "Chemical control in growing crops"; Dr. J. Stubbs (Visitor), "Wild Oats"; Mr. G. O. Lace of the Ministry of Agriculture, Fisheries and Food, Miss Olive Balme (Visitor), "The use of selective weedkillers in the control of vegetation on roadside verges"; and Mr. J. D. Fryer (Visitor), "The potential value of Herbicides for the selective control of vegetation in Nature Reserves".

In a general discussion the following also took part:—Lt.-Col. W. P. C. Tenison, Dr. E. B. Worthington, Dr. J. Ramsbottom, Dr. E. M. Delf, Dr. R. Melville, Mr. J. E. Lousley, and the President. **[Papers printed on p. 105.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 3 May 1957

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, and later Dr. John Ramsbottom, Past-President, in the Chair.

The President welcomed the presence of Professor Dr. Carl Skottsberg, Foreign Member, at the Meeting.

The Proceedings of the General Meeting held on 18 April 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—University of Washington Library, Mrs. M. F. Warner, Dr. Errol I. White, Dr. W. M. Curtis, Imperial College of Science and Technology, Dr. O. Hedberg, Dr. Knut Hagberg, Dr. B. M. Hobby and Dr. A. Tindall Hopwood.

Dr. Julian Rzóska signed the Obligation in the Roll and Charter Book, and was admitted a Fellow.

Certificates of Recommendation for Election to Fellowship were read for the first time in favour of:—Robert P. Celarier, M.S., Ph.D., Lewis Leonard Forman, B.Sc., A.L.S., William Devigne Russell Hunter, B.Sc., Ph.D. and William David Lindsay Ride, M.A., D.Phil., and a Certificate for an Associateship *honoris causa* was read for the first time in favour of Harry Barker.

Certificates of Recommendation for Election to Fellowship were read for the second time in favour of those candidates whose names appeared in the Minutes of the Meeting held on 18 April 1957.

The following were elected Auditors of the Treasurer's Accounts for 1956–57 under Chap. 10, Sect. 7 of the Bye-Laws.

For the Council: Mr. Peter R. Bell, Mr. D. Etherington.
For the Fellows: Mr. R. D. Meikle, Mr. R. H. Jeffers.

SYMPOSIUM ON CYTOTAXONOMY

A Symposium on Cyto-taxonomy was opened with an Introduction by Dr. W. B. Turrill; Mr. John L. Hamerton (Visitor), "Problems in Mammalian Cyto-taxonomy"; Dr. A. J. Cain, F.L.S., "Chromosomes and Taxonomic importance"; Dr. M. Fischberg (Visitor), "Effects of outcrossing on the Chromosome number in Vertebrates"; Dr. A. B. Acton (Visitor), "A cytological comparison of Nearctic and Palaearctic representatives of *Chironomus tentans* (Diptera)"; Professor Irene Manton, F.L.S., "Chromosomes and Fern Phylogeny"; Dr. T. G. Walker (Visitor), "The Cyto-taxonomy of a Tropical

Fern Complex (*Pteris quadriaurita* complex) " ; and Professor D. H. Valentine, F.L.S., " Cyto-taxonomy of the Rostrate Violets ".

In a general discussion on the following also took part :—Dr. R. E. Holttum, Mr. A. H. G. Alston, Mr. K. Jones, Dr. J. Ramsbottom, the President, Dr. J. Wilkinson, Dr. R. Melville, Mr. H. H. Crane and the Zoological Secretary ; Dr. Acton, Dr. Walker, Prof. Manton and Prof. Valentine replied. **[Printed in full on p. 110.]**

PROCEEDINGS OF THE ANNIVERSARY MEETING 24 May 1957

Dr. H. Hamshaw Thomas, M.B.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Friday, 3 May 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for the gifts made to the Library since the last Meeting :—Dr. B. M. Hobby, Dr. J. Ramsbottom, O.B.E., Mr. H. E. Hammond, Miss E. Ullmann, Mr. H. A. Hyde and Dr. W. R. Meade.

Miss Caroline Hobhouse was thanked for the gift of a Loadstone from the Mineral Collection of Linnaeus.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Thomas Douglas Victor Swinscow, M.R.C.S. (Eng.), L.R.C.P. (Lond.), M.B., B.S. ; Mrs. Edith Gertrude Thomas, M.A. ; Sydney Gerald Harrison, B.Sc. ; and Geoffrey Friyer B.Sc.

The President reported the deaths of Hugh Curtis Sampson, Walter Smithson Rowntree and Geoffrey Honorth Spencer Wood, Fellows, Auguste Chevalier, Foreign Member and Sir John Graham Kerr, Linnean Medallist, 1955.

Candidates for membership were balloted for and elected :—*Fellows :* K. C. Basu Chaudhary, M.Sc., Robert Gordon Darlington, Jagannath Dattatraya Kulkarni, B.Sc., B.Pharm., Ph.D., Samuel Frank Loring, M.A., Frederick Richard McQuown, M.A., and Donald Walker, B.Sc., M.A., Ph.D.

Associate honoris causa : Harry Barker.

Certificates of Recommendation for Election to Fellowship were read for the second time in favour of :—Robert P. Celarier, M.S., Ph.D., Lewis Leonard Forman, B.Sc., A.L.S., William Devigne Russel Hunter, B.Sc., Ph.D., and William David Lindsay Ride, M.A., D.Phil.

The Bye-Laws regulating the Election of Council and Officers having been read by the General Secretary, the President declared the Ballot for new Members of Council to be open, and voting began. The President thereafter appointed Mr. R. H. Jeffers, Mr. R. Ross and Mr. J. B. Gillett scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting. New Members of Council : Professor L. J. Audus, Mr. A. W. Exell, Dr. J. P. Harding, Mr. R. D. Meikle and Mr. H. L. G. Stroyan.

The retiring Councillors were Mr. J. S. L. Gilmour, Prof. C. T. Ingold, Dr. B. M. Hobby, Dr. L. Harrison Matthews, F.R.S. and Dr. George Taylor.

PRESENTATION OF LINNEAN GOLD MEDAL

In handing the Linnean Gold Medal to Dr. P. Brandberg, Director of the Swedish Institute, for onward transmission to Professor Erik Anderson Stensiö, who was unable to be present, the President said :—

Professor Erik Anderson Stensio, Keeper of the Palaeozoological Department of the Natural History Museum of Stockholm, is the outstanding

figure in palaeontology to-day, and certainly one of the greatest of all time. Although most of his work has been done on the lower vertebrates, his influence is widespread, for his first substantial work *The Triassic Fishes from Spitzbergen*, 1921–25 (2 volumes) at once created a new standard for palaeontological research. New and delicate methods of preparation revealed the anatomy in these ancient vertebrates comparable with that of living animals which his encyclopaedic knowledge of recent zoology allowed him to interpret with outstanding success. Perhaps even more important was his great memoir on the Downtonian and Lower Devonian "Cephalaspids of Spitsbergen". In this he showed for the first time the relationship of these ancient Devonian animals and their congeners the Pteraspids, with the living lampreys and hag-fishes. With remarkable industry, Professor Stensiö has produced no less than ten monumental monographs, several being in two volumes, on Devonian, Triassic and Cretaceous vertebrates, besides many smaller works, and further, his school of paleaontology has produced many outstanding figures in the field of Vertebrate Palaeontology.

It is good to know that Professor Stensiö and his colleagues are actively preparing a large series of works that are bound to be of fundamental interest.

PRESENTATION OF CRISP AWARD AND MEDAL

In handing the Crisp Award and Medal to Professor R. S. Adamson for onward transmission to Dr. Mary Agard Pocock, the President said :—

Dr. Mary Agard Pocock is an algologist of international reputation. She has travelled widely and has been blessed with the appreciative eye of the naturalist in her quest for algae, both fresh-water and marine. Her papers on members of the Volvocales indicate collections made in Berkeley California, Australia, New Zealand, India and Great Britain, as well as in South Africa where she has been a member of the staff of Rhodes University Grahamstown and the University of Cape Town.

Dr. Pocock has made important taxonomic contributions to algal literature, both in the Volvocales and the Rhodophyceae. She has added to our knowledge of the culture of the green algae as well as to their cytology. More recently she has studied Rhodophycean parasites and their hosts, a study for which the coast of South Africa is an especially rich habitat.

It is not only on account of her research however, that we welcome the opportunity of honouring Dr. Pocock to-day. She has spared no pains in helping students of all ages in their algal studies and she has given of her best to Universities and Colleges where she has worked. The lists of acknowledgments in her papers is an indication of the breadth of her friendships and of the wide fields in which she has given devoted service.

The Financial Report was given by the Treasurer and the Accounts of the Society, duly audited, for the year 1956–57 were laid before the meeting.

On a motion by Dr. Hugh Scott, F.R.S., seconded by Dr. R. E. Holttum, the Report and Statement of Accounts were adopted.

TREASURER'S REPORT

Printed copies of the accounts for the financial year which ended on 30 April 1957 are before you. For comparison, the figures for last year are printed in italics on the left-hand side. A Statement has been prepared by the Auditors who certify as to details ; the Audit Committee has inspected the books, verified the investments and bank balances and passed the Accounts ; the action of the Committee has been confirmed by the Council.

I will briefly go through the accounts and deal with the main items :—

Annual Contributions are higher due to last year's increase of subscriptions from £4 to £5. Thirty-four Fellows have taken advantage of the Special Composition Fee of £20 by instalments for those of 20 years standing who have reached the age of 65 and their Annual Contributions are included in the Composition Fees below ; of the total Fellowship of 830, 120 are Compounders.

Income Tax on Deeds of Covenant. We have a claim of £408 with the Inspector of Taxes. At the moment, however, claims of return of income tax of all societies paying subscriptions under Deed of Covenant are not being paid by the Inland Revenue Authorities pending a case in the Courts concerning subscriptions paid under Covenant.

Interest and Dividends are higher due to the higher Deposit Account Interest.

Composition Fees are again increased due to further Fellows, as mentioned above, having taken advantage of the Special Composition Fee.

Publications Sales amount to £1988, a record figure, and well above expected average receipts. This is due to the issue of the arrears of publications mentioned last year.

Grants for Publications. We are again very grateful to the Royal Society for their allocation of £1000 towards the cost of the Society's publications from the Parliamentary Grant-in-Aid for Publications."

A Legacy has been received of £200 from the Executors of Sir Sydney Harmer, a past President of the Society, which we acknowledge with gratitude.

On the Payment Side.

Electricity, Gas and Fuel. About the same although the costs have increased (the mild winter has prevented this figure being higher).

Furniture and Repairs. Is up a little due to replacement of worn parts in the Central Heating System, the purchase of 30 chairs to supplement the Meeting Room accommodation and sundry Furniture repairs and replacements.

National and Fire Insurance. Less due to the retirement of a member of staff.

Miscellaneous Printing and Stationery and Dispatch. Higher this year due to the increase in the cost of printing, stationery and printed matter postages.

Petty Expenses and Postages. Increase mainly due to postage on greatly increased sales and increase on inland postage on printed matter which was doubled.

Publications. The figure is lower than last year as it will be remembered that in the figure of last year was included the cost of printing in hand of the Journals which have since been issued.

The figure of this year includes the balance of the cost of the publications issued during the year and the cost of printing completed of publications in hand. Since the last Anniversary Meeting, 3 *Journals, Zoology*, 1 *Journal, Botany* and 3 parts of the *Proceedings* have been issued. Being printed at present are : 2 *Journals, Botany* (which includes the *Berberis* Monograph which we hope to issue this Session), 1 *Journal, Zoology* and *Synopsis of the British Fauna*, No. 11.

Transfer to Reserve for Publications. It has been possible to transfer the sum of £400 to this Reserve from this year's balance.

Also from the balance of this year's income the sum of £250 has been set aside towards the cost of next year's Darwin-Wallace Celebrations and £250 for redecoration and interior improvements.

Library Fund Account. The usual £500 have been transferred to meet the expenses of the Library.

Salaries, Wages and Pensions. This figure is higher than last year due to a Member of Staff going on Pension.

Investment of Composition Fees. There remains a balance of £12 awaiting investment.

The Library Fund.

The account has a balance of £126 after paying for the usual items. The figure for binding is much higher due to arrears of binding having been put in hand. It will be remembered that last year binding was restricted pending recommendations of the Library Committee regarding possibility of having several grades of binding.

Library Restoration Fund.

This Fund shows a balance of £1561 and it will be seen that we received a generous gift of £100 from His Majesty the King of Sweden for expenditure on the Society's Library, for which we are indeed grateful. We also received a most generous legacy of £1000 from our late Fellow, Mr. F. J. Barrington and the Council has decided that this will be expended on further repairs to the books from Linnaeus' Library. The Society has received only a small amount apart from the donation of His Majesty The King of Sweden and the legacy from Mr. Barrington. I should like to appeal again to all friends of the Linnean Society's Library to help this Fund—which I think is extremely important—in any way they can such as by donations or by legacies in order that this historic and valuable Library can be maintained and conserved as it should be.

Fellows' Postal Account.

This shows the deposits received and the expenditure of postage on books borrowed from the Library. It is of great assistance if Fellows will use this account rather than refund postage after each parcel.

Trust and Reserve Funds.

I have already mentioned the addition of the £400 to the Publications Reserve and the transfer towards the Darwin-Wallace Celebrations and the Interior Redecoration. Also there is shown a generous grant of £250 from the Royal Horticultural Society towards the cost of printing the *Berberis* Monograph.

Investments.

During this year the Society encashed £1000 2½ per cent Defence Bonds at par, they reinvested £500 of this sum and £500 Composition Fees received in 4½ per cent Defence Bonds at par. The remaining £500 is on deposit awaiting investment in suitable equities.

The Council has decided that to simplify matters for the Auditors and Printers, the Society's Financial Year will in future end on 31 March. Thus for this coming year the Accounts will cover 11 months' expenditure.

I should like to thank our General Secretary, Mr. T. O'Grady and our Clerk, Mrs. Edith Ziegler, for the excellent way in which the accounts have been kept, and for the conscientious way in which the work has been done.

If any Fellow wishes to ask any questions on these accounts, I will do my best to answer them.

TREASURER'S ACCOUNTS FOR THE
(Presented at the Anniversary
Receipts and Payments of the Linnean Society

General

1955–56 £	RECEIPTS	£ s. d.	1956–57 £ s. d.
	To Balance at 1 May 1956 :—		
	Current Account at Bank	219 10 4	
	Deposit Account at Bank	500 0 0	
	Deposit Account Post Office Savings Bank	209 7 6	
	Cash in hand	11 0 7	
811			939 18 5
64	,, Admission Fees		60 0 0
	,, Arrears of Annual Contributions	60 16 0	
	,, Annual Contributions for year	3244 14 5	
	,, in advance	121 11 8	
3020			3427 2 1
22	,, of Associates		35 0 0
308	,, Income Tax recovered on Deeds of Covenant		—
336	,, Composition Fees		488 0 0
418	Interest and Dividends (including Income Tax recovered)		539 1 3
122	Post Office Savings Bank Account		50 3 6
	Sales of Publications :—		
	Transactions	63 0 9	
	Journals	1630 16 5	
	Proceedings &c.	294 11 8	
1033			1988 8 10
	,, Grants in aid of Publications :—		
1250	Royal Society	1000 0 0	
10	*Queen Mary College*	—	
625	*Percy Sladen Memorial Fund*	—	
			1000 0 0
—	,, Sir Sidney Harmer—Legacy		200 0 0
4	,, Sundry Donations		17 18 0
115	,, Miscellaneous Receipts		137 12 9
25	,, Fellows' Postal Account		—
—	,, Transfers from Trust Funds :—		
2250	Reserve for Publications	—	
500	Auckland Univ. Grant (Chapman)	—	
—	,, Encashment of £1000 *22* per cent Defence Bonds		1000 0 0
10913			£9883 4 10

Library

£ s. d.		£ s. d.
91	To Balance at 1 May 1956	144 4 3
79	,, Interest on Investments (including Income Tax recovered)	78 17 3
10	,, Donations : John Innes Horticultural Institution 10 10 0	
21	Imperial Chemical Industries Ltd. 21 0 0	
		31 10 0
500	,, Transfer from General Account	500 0 0
701		£754 11 6

Library

£ s. d.		£ s. d.
723	To Balance at 1 May 1956	729 7 3
—	,, Donations : H.M. King of Sweden 100 0 0	
—	F. J. F. Barrington—Legacy 1000 0 0	
6	Fellows 10 0	
		1100 10 0
729		£1829 17 3

Fellow's Postal

£		£ s. d.
50	To Balance at 1 May 1956	24 6 2
—	,, Deposit	6 5 0
50		£30 11 2

YEAR ENDED 30 APRIL 1957

Meeting, 24 May 1957)

from 1 *May* 1956 *to* 30 *April* 1957.

Account

1955–56 £	PAYMENTS	£ s. d.	1956–57 £ s. d.
256	By Electricity, Gas and Fuel		255 6 8
158	,, Furniture and Repairs		200 6 8
102	,, National Insurance and Fire Insurance		91 19 8
422	,, Miscellaneous Printing and Stationery and Dispatch		490 5 1
425	,, Petty Expenses and Postages		489 5 1
	,, Publications (including payment on account) :—		
	Printing	1962 9 2	
	Distribution	48 5 7	
	Illustrations	79 7 8	
4987			2090 2 5
174	,, Stockroom Reorganization		—
	,, Transfer to Reserve for Publications Fund	400 0 0	
	,, ,, Darwin-Wallace Celebrations, 1958	250 0 0	
	,, ,, Redecoration and improvements	250 0 0	
			900 0 0
750	,, Transfer to Reserve for *Berberis* Monograph		—
500	,, Transfer to Library Accounts		500 0 0
1894	,, Salaries, Wages and Pensions		2027 14 3
15	,, Donations : Zoological Record	15 0 0	
4	Internation Union for Nature Protection	2 2 0	
—			17 2 0
4	,, International Assoc. for Plant Taxonomy—Subscription		7 0 0
71	,, Staff Annuities (Annual Premiums)		58 0 0
184	,, Investment of Compounders' Fees		500 0 0
28	,, Linnean Medal		21 12 6
—	,, Darwin-Wallace Celebration Medals, 1958		157 12 0
—	,, Purchase of £500 4½ per cent Defence Bonds		500 0
	,, Balance at 30 April 1957 :—		
	Current Account at Bank	174 17 10	
	Deposit Account at Bank	1100 0 0	
	Deposit Account Post Office Savings Bank	259 11 0	
	Cash in hand	42 9 8	
939			*1576 18 6
10913			£9883 4 10

*Includes £12 balance of Composition Fees to be invested after deduction of Fees of deceased Compounders, and £500 proceeds of sale of 2½% Defence Bonds awaiting re-investment.

Account

£		£ s. d.
293	By Periodicals	222 8 0
168	,, Binding	325 13 6
96	,, Books	80 6 1
	,, Balance at 30 April 1957 :—	
144	Current Account	126 3 11
701		£754 11 6

Restoration Fund

£		£ s. d.	£ s. d.
—	By Rebinding Linnean Books		268 0 0
	,, Balance at 30 April 1957 :—		
	Current Account at Bank	182 12 9	
	Deposit Account at Bank	762 10 6	
	Deposit Account Post Office Savings Bank	616 14 0	
729			1561 17 3
729			£1829 17 3

Account

£		£ s. d.
1	By Postage on Library Books	1 11 6
25	,, Transfer to General Account	—
24	,, Balance 30 April 1957	28 19 8
50		£30 11 2

Special Accounts

(Trust and Reserve Funds

Receipts	£ s. d.	£ s. d.
To Balance at 1 May 1956 :—		
Westwood Fund	91 1 2	
Trail Award Fund	8 5 9	
Crisp Award Fund	83 14 1	
Hooker Lecture Fund	149 19 7	
Goodenough Fund	40 16 9	
Minchin Fellowship Fund	1 10 5	
Carnegie Corporation Grant	419 3 7	
Reserve for Publications Fund	1740 5 3	
Grant for *Berberis* Monograph (Royal Society)	750 0 0	
		3284 16 7
,, Grant for *Berberis* Monograph (Royal Horticultural Society)		250 0 0
,, Transfer from General A/c for :—		
Publications Reserve Fund		400 0 0
Darwin - Wallace Celebrations, 1958	250 0 0	
Redecoration and improvements	250 0 0	
		900 0 0
Interest on Investments (gross) :—		
Westwood Fund	10 17 4	
Trail Award Fund	3 11 4	
Crisp Award Fund	13 19 0	
Hooker Lecture Fund	21 18 0	
Goodenough Fund	8 12 8	
Minchin Fellowship Fund	3 0 0	
Staff Pension Fund	10 8 11	
		72 7 3
		£4507 3 10

Payments	£ s. d.	£ s. d.
By Staff Pension Fund :—		
Purchase of £11 12*s.* 10*d.* 3 per cent Savings Bonds 1955–65		10 8 11
,, Balance at 30 April 1957 :—	£ s. d.	
Westwood Fund	101 18 6	
Trail Award Fund	11 17 1	
Crisp Award Fund	97 13 1	
Hooker Lecture Fund	171 17 7	
Goodenough Fund	49 9 5	
Minchin Fellowship Fund	4 10 5	
Carnegie Corporation Grant	419 3 7	
Reserve for Publications Fund	2140 5 3	
Grant for *Berberis* Monograph (Royal Society)	750 0 0	
Grant for *Berberis* Monograph (Royal Horticultural Society)	250 0 0	
Darwin-Wallace Celebrations 1958	250 0 0	
Redecoration and improvements Reserve	250 0 0	
		*4496 14 11
		£4507 3 10

* Including £181 5*s.* 10*d.* in Post Office Savings Bank and £3000 Deposit Account at Bank.

Investments on 30 *April* 1957

£	s.	d.			Market value 30 *April* 1957 £	s.	d.
			General Account				
1000	0	0	3½ per cent London County Consolidated Stock 1958–68	@ 86	860	0	0
1548	8	9	British Transport 3 per cent Guaranteed Stock 1978–88	@ 70½	1091	11	10
1172	6	3	3½ per cent War Loan, 1952 or after	@ 71½	838	4	1
500	0	0	2½ per cent Defence Bonds	@100	500	0	0
2199	18	6	4 per cent Australia Stock 1961–64	@ 91½	2012	18	7
200	0	0	3 per cent War Stock 1955–59	@ 97	194	0	0
1139	13	0	3 per cent Savings Bonds 1955–65	@ 87½	997	3	11
3260	1	3	2½ per cent Consolidated Stock	@ 53½	1744	2	8
176	19	3	3 per cent Savings Bonds 1960–70	@ 79½	140	13	8
274	5	5	3 per cent Treasury Stock	@ 62½	171	8	4
500	0	0	4½ per cent Defence Bonds	@100	500	0	0
					£9050	3	1
			Library Account				
471	18	9	British Transport 3 per cent Guaranteed Stock 1978–88 (Bentham Bequest)	@ 70½	332	14	1
103	12	5	Surrey County 3 per cent Stock 1961–66 (Wakehurst Bequest)	@ 83	86	0	11
191	12	7	4 per cent Australia Stock 1961–64 (Walker & Morey Bequests)	@ 91½	175	6	10
107	2	1	2½ per cent Consolidated Stock (Stebbing Bequest)	@ 53½	57	6	0
530	0	0	3 per cent Savings Bonds 1960–70 (Tagart Bequest)	@ 79½	421	7	0
1414	7	11	2½ per cent Consolidated Stock (Flintoff Bequest)	@ 53½	756	14	1
					£1829	8	11
			Special Accounts				
232	5	0	Metropolitan Water Board 3 per cent " B " Stock (Westwood Bequest)	@ 65½	152	2	6
667	14	2	,, ,, (Hooker Lecture Fund)	@ 65½	437	6	11
163	11	5	,, ,, (Goodenough Fund)	@ 65½	107	2	9
557	12	1	2½ per cent Consolidated Stock (Crisp Award Fund)	@ 53½	298	6	4
156	7	2	,, ,, (Westwood Fund)	@ 53½	83	13	1
74	14	6	,, ,, (Hooker Lecture Fund)	@ 53½	39	19	7
149	8	10	,, ,, (Goodenough Fund)	@ 53½	79	19	0
345	4	10	3 per cent Savings Bonds 1955–65 (Staff Pension Fund)	@ 87½	302	1	9
12	0	10	,, ,, ,, 1955–56 (Staff Pension Fund)	@ 87½	10	10	9
100	0	0	,, ,, ,, 1960–70 (Minchin Fund)	@ 79½	79	10	0
102	3	11	3½ per cent War Loan 1952 or after (Trail Award Fund)	@ 71½	73	1	5
			F. C. STERN, *Treasurer.*		£1663	14	1

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1957 and found them correct. We have verified the Investments and Bank Balances.

15 May 1957.

W. B. KEEN & Co., *Chartered Accountants,*
Finsbury Circus House, Blomfield Street, London, E.C.2.

H. HAMSHAW THOMAS,
H. R. HEWER,
C. R. METCALFE
R. D. MEIKLE
ROBERT H. JEFFERS
PETER R. BELL
Audit Committee.

GENERAL SECRETARY'S REPORT

List of the Society.

Since the last Anniversary Meeting the Society has lost 37 members. The detailed statement is as follows:—

12 *Fellows by Death:*

Miss Lucy Ellen Cox.
Henry James Howard.
Cecil Prescott Hurst.
John Withers Lester.
Arthur Mayfield.
William Marshall.
Henry Nicholas Ridley.
Walter Smithson Rowntree.
Hugh Curtis Sampson.
Sir William Wright Smith.
His Honour Judge H. Drysdale Woodcock.
Geoffrey Honorth Spencer Wood.

2 *Foreign Members by Death:*

Auguste Chevalier.
David Fairchild.

1 *Associate honoris causa:*

Benjamin Storrow.

17 *Fellows by Withdrawals:*

Sir Eric Ashby.
Frederick John Aumonier.
Frederick Bond.
Thomas Archibald Bennet-Clark.
Sydney Challenger.
Cyril Bibby.
Miss Honor Bridget Fell.
Cecil Miles.
Miss Eleanor Mary Ord Laurie.
George Donaldson Lockie.
David Richmond Newth.
John Dean Palmer.
Sidney Robert Brown Pask.
James Philip Cuming Russell.
Clifford Charles Townsend.
John Vardy.

5 *Fellows by Removal for Non-payment of Annual Contributions in Accordance with Bye-Laws, Chap. 2, Sect. 4:*

Felix Oladijo Dosekun.
Abdus Sattar Khan.
A. S. G. Mardon.
Promode Kumar Sanyal.
Ernest Rouleau.

During the Session 29 Fellows, 1 Associate *honoris causa* and 3 ordinary Associates have been elected. The number of Fellows on the List is 832, with a further 13 Fellows elected but still to qualify; 48 Foreign Members; 25 Associate *honoris causa* and 29 ordinary Associates. Three ordinary Associates have withdrawn during the year, of whom one Associate has been elected Fellow.

The Library.

Between 1 May 1956 and 30 April 1957, 22 books have been purchased; 41 books, 78 parts of periodical publications and 132 reprints have been presented. During the same period the number of volumes bound was 309; the number of volumes borrowed was 483. Six hundred and forty-one signatures were recorded in the Library Visitors' Book.

Many meetings of other Societies continue to be held in the Society's Rooms.

The PRESIDENT declared the Ballot for Officers to be open and voting began. The Ballot was closed at the due time, and the result declared to the Meeting: *President:* Dr. H. Hamshaw Thomas, M.B.E., F.R.S.; *Treasurer:* Sir FREDERICK STERN, O.B.E., M.C.; *Zoological Secretary:* Mr. H. R. HEWER, M.Sc.; *Botanical Secretary:* Dr. C. R. METCALFE.

The PRESIDENT gave his Annual Review of the Society's activities.

THE PRESIDENT'S REVIEW

Although our Anniversary Meeting this year is not the last General Meeting of the Session, we may look back on the events of the past year, the 169th in the history of the Society, with some satisfaction. At the outset there were anxieties as to the future. We had increased the Annual Contribution payable by Fellows; our Meetings had been criticized from several different quarters, and we were faced with problems in the Library. But our numbers have been fairly well maintained, our General Meetings have been very well attended and our arrangements for the Library have worked efficiently.

One outstanding event of the year, in which we celebrate the 250th anniversary of the birth of Linnaeus, has been the visit of His Majesty Gustav VI Adolf, King of Sweden. Since about 1888 the Kings of Sweden have accepted the Honorary Membership of our society, but it is very doubtful if any previous monarch has shown such interest and knowledge as were displayed by King Gustav on 17 April 1957. It was very gratifying that he expressed a desire to visit our rooms and to see our collections, and he spent more than an hour here with as many representatives of the Officers and Council as could be collected together at short notice. He signed his name in our Roll and Charter Book, and examined very thoroughly all the exhibits that had been arranged for his inspection. These were selected from the books, manuscrips and collections of Linnaeus. He was especially interested in the carved Rhinoceros horn which had belonged to Linnaeus, and is of oriental origin; he asked that photographs of the beautiful object might be sent to him. On leaving he kindly promised a donation of £100 for our Library Fund, to assist us in safeguarding the Linnaean books and Manuscripts.

During the past year eleven General Meetings have been held, and it is proposed to hold an additional meeting next July as an experiment. It had been represented to the Council that a meeting at this time of the year might be popular with Fellows who find difficulty in attending our ordinary meetings. The Council have also proposed an alteration in the Bye-Laws by which it becomes possible for General Meetings to be held on days other than the customary Thursdays from time to time. This alteration was submitted to the Fellows and approved. It will enable special meetings to be held on Friday or Saturday, when Fellows can more easily come to London from the provinces. The first meeting of this kind was a symposium on Cyto-taxonomy held at 11.15 a.m. on 3 May. It was well attended, several of the speakers, and members of the audience, came from the north of England for the occasion.

Other symposia have been devoted to subjects of biological importance with a practical application, viz. Aerobiology, Weed-killers, and Nematoda parasitic on plants. At a joint meeting with the Systematics Association the present position with regard to the Inheritance of Acquired Characters was discussed. Two meetings were devoted to accounts of plants and animals in interesting areas of the world, both illustrated with very beautiful pictures. Under the title of "Return to the collecting grounds of Richard Spruce", Dr Bassett Maguire, a visitor from America, described his recent exploration in the Headwaters of the Rio Orinoco and Rio Negro, South America, illustrated by a

remarkable colour film. Sir Frederick Stern and Mr. Milne-Redhead on another evening gave beautifully illustrated accounts of vegetation in South Africa and in Southern Tanganyika. Other visitors kindly gave us accounts of the Seal islands of Alaska and Uruguay. Among those visitors who have contributed to our meetings our thanks are especially due to the Director and Staff of the Fisheries Laboratory, Lowestoft, for an account of some of the research work which is being carried out at their station. We have also had some excellent papers read by our Fellows which gave rise to interesting discussions.

The evening reception was held on 6 December, when there was a large gathering of Fellows and their friends. Our rooms were beautifully decorated with plants kindly lent by the Director of the Royal Botanical Gardens, Kew, and with fine carnations and chrysanthemums provided by the generosity of Mr. F. O. Mosley, one of our Fellows. Many interesting exhibits were on view and our thanks are due to all those who provided and arranged them. During the evening a remarkably interesting film, depicting the Grey Seal of the Hebrides, was shown by Prof. H. R. Hewer, our Zoological Secretary.

Our celebration of the birth of Linnaeus will be held on 30 May, and will take the form of an evening party at which His Excellency the Swedish Ambassador has kindly promised to speak on "Sweden in the time of Carl Linnaeus", and Mr. W. T. Stearn, F.L.S., will talk about the botanical exploration of the world before the journeys of the pupils of Linnaeus. These lectures will provide the historical background which is so essential to a complete appreciation of the man and his achievements. Some of the more interesting books, manuscripts and specimens from our Linnaean Collections will be on view. We are very grateful to the Geological Society for allowing us to use their Meeting Room on this occasion.

The Society will be represented at the anniversary celebrations in Uppsala by Dr. W. B. Turrill, and Dr. Ramsbottom will represent us at the functions arranged by the Linnean Society of Sweden. Major A. R. Tainsh, F.L.S., will act as our delegate at the ceremonies which are arranged for to-day at Rashult and Stenbrohult, the places where Linnaeus was born and brought up.

It gives me particular pleasure to report that we have recently received a valuable addition to the Linnaean Collections. As is well known Sir James Edward Smith acquired the entire Collections of Linnaeus, but he disposed of the rocks, minerals and fossils; he retained, however, a fine mounted loadstone with its keeper. This interesting specimen eventually came into the possession of Miss Caroline Hobhouse who has presented it to the Society.

Fellows may like to know that a Meeting of the Junior Members of the Botanical Society of the British Isles was held in our rooms on 5 January 1957 and a meeting of the Anglo-Swedish Society on 2 April 1957. On both occasions your President gave some account of the life and work of Linnaeus, and specimens from the Collections were exhibited.

Our plans for the celebration of the Darwin-Wallace Centenary on 16 July next year, in conjunction with the Royal Society and the Geological Society, are taking shape. We hope to hold a special meeting on 15 July 1958 to commemorate the bicentenary of the publication of the *Systema Naturae* of Linnaeus.

We have lost a number of Fellows by death during the year, among whom I should like to mention our oldest Fellow, Mr. H. N. Ridley, Sir William Wright Smith, and two of our Foreign Members, David Fairchild and Auguste Chevalier. Sir John Graham Kerr, a former fellow and Linnean Medalist for 1955, must also be remembered.

Your Council has spent a considerable amount of time in discussing the position of the Library. Mr. B. Wislawski has been appointed Assistant Librarian, but it is felt that for a Library as large and important as ours a

Librarian with special training and qualification is needed. At the present time we cannot set aside annually the sum of money that would be necessary to pay the salary of such a person, and some alternative may have to be found.

Our library includes nearly 400 periodicals, purchased or received in exchange and a number of these are not available elsewhere, but since 1939 it has been necessary to discontinue no less than 43 German periodicals, which were formerly purchased, and to most of which the Society had subscribed since their commencement. It is felt that this leaves a very serious gap on our shelves, but the cost of renewing our subscriptions and obtaining the missing parts is so great that it cannot now be contemplated.

Our Library is a national asset and we feel that efforts should be continued to obtain financial assistance for its maintenance from sources outside the Society. At the present time when the importance of science to the nation is being so widely stressed, there ought to be a wider appreciation of the part played by scientific societies like ours in the progress of science in Britain. We play an essential role in the promotion of scientific research and in the publication of results, and this work is worthy of public support.

I am very glad to be able to report that the serious arrears in the publication of our journals have been almost made up during the year and by the distribution to-day of the Proceedings up to the last anniversary meeting.

We must especially thank Mr. N. Y. Sandwith and Mr. W. H. T. Tams for their work as Curators of the Linnaean Collections. During this year their Office has been by no means a sinecure, and they have done valuable work in selecting specimens for exhibition on the occasions when exhibits have been shown. May I take this opportunity of pointing out that some parts of the Linnaean Collections need further attention. Many of the molluscan shells in the collection are virtually in the condition in which they were received nearly 130 years ago from the executors of Sir James Edward Smith. They badly need cleaning and putting in order. In my view the Linnaean Manuscripts also need attention, and their storage in fireproof containers should be considered.

Finally I wish to express our thanks to our Treasurer and our Secretaries for all the work that they have done for the Society. Their duties have been unusually heavy during the past year. May I also thank the Members of the Council and Library Committee for devoting their time and thought to the many problems we have to face.

The PRESIDENT then delivered his Address, "Palaeobotany and the Evolution of the Flowering Plants".

On its conclusion, Dr. J. Ramsbottom, O.B.E., moved, "That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows". The motion was seconded by Prof. C. T. Ingold, and being put to the meeting was carried with acclamation. **[Address printed on p. 134.]**

The President announced that he had appointed the following as Vice-Presidents for 1957–58: Dr. C. F. A. PANTIN, F.R.S., Sir FREDERICK STERN, O.B.E., M.C., Dr. ERROL WHITE, F.R.S., and Miss E. M. WAKEFIELD, O.B.E.

The following papers were read in title :—

MARCUS, E. On Opisthobranchia from Brazil. **[Printed in *Journal, Zoology*, No 292.]**

UVAROV, B. P. & POPOV, G. B. The saltatorial Orthoptera of Socotra. **[Printed in *Journal, Zoology*, No. 292.]**

BURT, D. R. R. & EADIE, I. M. *Cyathosoma lari* Blanchard 1849 (Nematoda, Strongyloidea); its anatomy, intra-specific variation and hosts, with a re-definition of the genus. **[Printed in *Journal, Zoology*, No. 293.]**

STROYAN, H. L. G. A contribution to the Taxonomy of some British species *Sappaphis* Matsumura (Homoptera, Aphidoidea). **[Printed in *Journal, Zoology*, No. 294.]**

BLOWER, J. G. British Millipedes (Diplopoda) with keys to the species. **[Printed in *Synopses of the British Fauna*, No. 11.]**

POPOV, G. B. The Vegetation of Socotra. **[Printed in *Journal, Botany*, No. 362.]**

ROUND, F. E. The Diatom Community on some Bryophyta growing on sandstone. **[Printed in *Journal, Botany*, No. 362.]**

ROUND, F. E. A note on some Diatom Communities in Calcareous Springs and Streams. **[Printed in *Journal, Botany*, No. 362.]**

MORRISON, G. D. Thysanoptera from South-west Arabia and from Ethiopia. **[Printed in *Journal, Zoology*, No. 293.]**

FOX, M. A first list of Marine Algae from Nigeria. **[Printed in *Journal, Botany*, No. 362.]**

DUCKE, A. The genus *Manilkara* Adans. in Brazil as seen by a field botanist. **[Printed in *Journal, Botany*. No. 362.]**

BATE-SMITH, E. C. & METCALFE, C. R. Leuco-anthrocyanins. 3. The nature and systematic distribution of tannins in dicotyledonous plants. **[Printed in *Journal, Botany*, No. 362.]**

GRIFFITH, M. A revision of the African species of *Terminalia*. **[Printed in *Journal, Botany*, No. 364.]**

DE BEER, Sir Gavin. The Dick Herbarium: Additional Note. **[Paper printed on p. 143.]**

ADDITIONS AND GIFTS TO THE LIBRARY

1956–57

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

Acta. Societatis Zoologicae Bohemoslovenicae. Vol. 1→ 8vo. *Praha*, 1917→
Acta Universitatis Szegediensis. Acta Botanica. Vol. 4→ 8vo. *Szeged*, 1949→
Ahmad, Nazir. Transplantation of Food Fish in East Pakistan. (Repr. Pakistan J. Sci., vol. 8, 1956.) [Author.]
— — Paddy-Cum-Fish Culture. (Repr. Agric. Pakist., vol. 7, 1956.) [Author.]
— — Fish Markets of East Pakistan and the Question of Their Improvement. [Author.]
— — Certain Observations on the Spawning of Major Carps in the River Halda of Chittagong (East Pakistan). (Repr. J. Zool. Soc. India, vol. 7, 1955.) [Author.]
— — Fishing with the Hand in East Pakistan. (Repr. J. Zool. Soc. India, vol. 6, 1954.) [Author.]
Allen, George H. Age and Growth of the Brook Trout in a Wyoming Beaver Pond. (Repr. Copeia, No. 1, 1956.)
American Geographical Society. *See* **Haden-Guest, Stephen, Wright, John K. & Teclaff, E. M.**
Anderson, Donald B. *See* **Meyer, B. S. & Anderson, Donald B.**
Aquila. Madartani Intezet. (Annales Instituti Ornithologici Hungarici.) Vol. 59→ 8vo. *Budapest*, 1952→
Archiv der Freunde der Naturgeschichte in Mecklenburg. Vol. 1→ 8vo. *Rostock*, 1954→
Archivos del Instituto de Aclimatacion. Vol. 1→ 8vo. *Almeria*, 1953→
Armitage, Eleonora. A Short Account of the Moss Exchange Club and the British Bryological Society. 1956. [Author.]
Ax, Peter. Monographie der Otoplanidae (Turbellaria). Morphologie und Systematik. Pp. 298. 8vo. *Wiesbaden*, 1956.
Axell, H. E. Predation and Protection at Dungeness Bird Reserve. (Repr. Brit. Birds, vol. 49, 1956.) [Nature Conservancy.]

Bailey. The Liberty Hyde Bailey Hortorium at Cornell University. A Story in pictures.
Baschieri, Francesco. *See* **Roghi, Gianni & Baschieri, Francesco.**
Berg, Kaj & Petersen, Ib Clemens. Studies on the Humic, Acid Lake Gribsø. Pp. 273. 8vo. *Copenhagen*, 1956. [Director Freshwater Biol. Lab., Univ. Copenhagen.]
Berrill, H. J. The Origin of Vertebrates. Pp. viii + 257. 8vo. *Oxford*, 1955.
Bilham, E. G. The Climate of the British Isles. Pp. xix + 347. 8vo. *London*, 1938. [F. J. F. Barrington Bequest.]
Biologia. (Published by Slovak Academy of Science.) Vol. 6→ 8vo. *Bratislava*, 1951→
Biologické Prace. (Published by Slovak Academy of Science.) Vol. 1→ 8vo. *Bratislava*, 1955→
The Birds of the London Area Since 1900. (New Naturalist Series.) Pp. x + 305. 8vo. *London*, 1957.
Bogdan, A. V. Indigenous Clovers of Kenya. (Repr. East African Agric. J., vol. 22, 1956.) [Author.]
Boletin del Instituto Espanol de Oceanografia. No. 69.→8vo. *Madrid*, 1955→
Borbásia. Acta Societatis Botanicorum Hungaricae. Vols. 1–9. 8vo. *Budapest*, 1938–49.
Brian, M. V. Group Form and Causes of Working Inefficiency in the Ant *Myrmica rubra* L. (Repr. Physiol. Zoology, vol. 29, 1956.) [Nature Conservancy.]
— — Studies of Caste Differentiation in *Myrmica rubra* L. 4. Controlled Larval Nutrition. [Nature Conservancy.]
— — **& Brian, A.D.** On the Two Forms Macrogyna and Microgyna of the Ant *Myrmica rubra* L. (Repr. Evolution, vol. 9, 1955.) [Nature Conservancy.]
Brien, Paul. La Génétique et les Théories de Lyssenko. (Repr. Bull. l'Union Anciens Etud. de l'Université Libre de Bruxelles, No. 175, 1949.) [Author.]
Bulletin of the Botanical Society of Bengal. Vol. 2→ 8vo. *Calcutta*, 1947→
Burt, W. V. *See* **Rattray, M. & Burt, W. V.**

Calpouzos, Lucas. Studies on the Sigatoka Disease of Bananas and its Fungus Pathogen. (Atkins Garden and Res. Lab., 1955.) [Mr. R. H. Hudson.]
Carlsberg Foundation. *See* **Pedersen, Johannes.**
Chandra, V. Studies on *Rauwolfia*. Pts. 1–5. (Repr. Indian J. pharmacy, vol. 18, 1956.) [Director National Bot. Gardens, Lucknow.]
Charles, W. N. The Effects of a Vole Plague in the Carron Valley, Stirlingshire. (From Scottish Forestry.) [Nature Conservancy.]
Chelsea Physic Garden. Library Catalogue. Pp. 35. 8vo. *London*, 1956. [City Parochial Foundation.]
Cobley, Leslie S. An Introduction to the Botany of Tropical Crops. Pp. xv + 357. 8vo. *London*, 1956. [Publishers.]
Convay, Verona M. The Moor House National Reserve Westmorland. (Repr. Soc. Promotion Nature Reserves Handbook, 1955.) [Nature Conservancy.]
Cook, W. R. Ivimey. *See* **McLean, R. C. & Cook, W. R. Ivimey.**
Corbet, A. Steven & Pendlebury, H. M. The Butterflies of the Malay Peninsula. Ed. 2. Pp. xi + 537. 8vo. *London*, 1956. [Dr. B. M. Hobby.]
Culpeper, Nicholas. The Complete Herbal. Pp. x + 603. 8vo. *Birmingham*, 1953. [F. J. F. Barrington Bequest.]
Curtis, Winifred M. The Student's Flora of Tasmania. Part 1. Pp. xlvii + 240. 8vo. *Tasmania*, 1956. [Author.]
da Costa, Antonio & Stern, Joseph A. The Calcium and Phosphorus Contents of some Foreign and Domestic Canned Sardines. (Repr. Food Research, vol. 21, 1956.)

Dahl, Jørgen. *Orthocladius Naumanni* Brundin (*Dipt. Chiron.*), New to Denmark, with Description of the Female. (Repr. Ent. Medd., vol. 26, 1954.) [Freshwater Biol. Lab., Univ. Copenhagen.]
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Dunn, D. Rowan. Notes on the Bottom Fauna of twelve Danish Lakes. (Repr. Vidensk. Medd. fra Dansk naturh. Foren., vol. 116, 1954 [Freshwater Biol. Lab. Univ. Copenhagen.]
Dupuis, Claude. Bibliographie des Travaux Entomologiques de Marcel Caruel (1893-1955) avec une Introduction Biographique. (Repr. Cahiers des Naturalistes, Bull. N.P., n.s. 11, 1955.) [Hope Dept. of Entomol. Univers. Museum, Oxford.]

Edney, E. B. The Water Relations of Terrestrial Arthropods. Pp. vi + 109. 8vo. *Cambridge*, 1957.
Elliott, R. J. Nature Reserves in the North of England with special reference to Roudsea Wood National Nature Reserve. (Repr. Soc. for Protection of Nat. Reserves Handbook, 1956.)

Fauvel, Pierre. The Fauna of India. Polychaeta. Pp. xii + 507. 8vo. *Allahabad*, 1953.
Felsko, Elsa. A Book of Wild Flowers. Pp. xi + 231. 8vo. *Oxford*, 1956. [Publishers.]
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Ford, E. B. Butterflies. 3rd ed. Pp. xiv + 368. 8vo. *London*, 1957.

Galliford, A. L. Notes on the Ecology of Pools in the Salt Marshes of the Dee Estuary. (Repr. Liverpool Nat. Field Club. Proc., 1955.) [Author.]
— — Rotifera of Lancashire and Cheshire. Report Nos. 2 and 3. (Repr. Report Lancashire & Cheshire Fauna Comm., 1948–49, 1950–53.) [Author.]

George, R. S. A Synopsis of the Information available concerning Dictyoptera, Orthoptera and Dermaptera in Gloucestershire. (Repr. Proc. Cotteswold Nat. Fld. Cl., 1953.) [AUTHOR.]

— — Some Additional Records of Arachnida from Gloucestershire, including four Species of Mites New to Great Britain. (Repr. Ent. Mon. Mag., vol. 91, 1955.) [AUTHOR.]

— — Some Records of Acrididae (*Orthoptera*) from the MSS. of the late E. J. Clark. (Repr. Ent. Gaz., vol. 6, 1955.) [AUTHOR.]

— — Siphonaptera from Gloucestershire, 1. (Repr. Ent. Gaz., vol. 5, 1954.) [AUTHOR.]

— — Siphonaptera from Gloucestershire, 2. (Repr. Ent. Gaz., vol. 6, 1955.) [AUTHOR.]

— — Siphonaptera from Gloucestershire, 3. (Repr. Proc. C.N.F.C., vol. 32, 1954.) [AUTHOR.]

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BENEFACTIONS

1955–56

LIST *in accordance with Bye-Laws, Chap* 17, *Sect.* 1, *of all Donations of the amount or value of Twenty pounds and upwards, received during the past five years.*

1952

The Royal Society : Grant-in-aid of publications, £1250.
The John Innes Horticultural Institution ; Gift to Library Fund (£10, 1950, 1951 and 1952), £30

1953

Auckland University College : Grant towards cost of Prof. V. J. Chapman's paper on New Zealand Algae in *Journal, Botany* (press), £500.
The Royal Society : Grant-in-aid of publications, £950.
Mr. J. D. Snowden : Gift towards cost of paper on *Sorghum* in *Journal, Botany* (press), £25.
Gift to Library Fund in Memory of Miss Maud Williams, F.L.S., £100.
Dr. Hugh Scott, F.R.S. : Cost of blocks for plates and £93 0*s*. 11*d*. towards cost of printing his Gughé Highlands' paper in *Proceedings*, 163.

1954

Mr. H. Womersley, A.L.S. : Gift towards cost of paper in *Journal, Zoology*, No. 288, £20.
Imperial Chemical Industries Limited : Gift to Library Fund, £21.
The Royal Society : Grant-in-aid of publications, £100.
Mr. A. A. Pearson, F.L.S. : Bequest of Myological Library.

1955

The Royal Society : Grant-in-aid of publications, £1250.
The Percy Sladen Memorial Fund, Cost of printing *Transactions*, Ser. 3, Vol. 1, Part 3, £625 3*s*. 6d.
Imperial Chemical Industries Limited : Gift to Library Fund, £21.
The John Innnes Horticultural Institution : Gift to Library Fund (£10 1953, 1954 and 1955), £30.

1956

The Royal Society : Grant-in-aid of publications, £1000.
Mr. F. J. F. Barrington, F.L.S. : Legacy of £1000.
Sir Sidney F. Harmer, K.B.E., F.R.S., P.P.L.S. : Legacy of £200.
The Royal Horticultural Society : Grant of £250 towards the cost of the *Berberis* Monograph to be issued in the Society's *Journal, Botany*.
Imperial Chemical Industries Limited : Gift to the Library Fund, £21.

OBITUARIES

Henry Nicholas Ridley (1855–1956) was the second son (third child) of Oliver Matthew Ridley, Clerk in Holy Orders, and his wife Louisa Pole née Stuart. At the date of his birth—10 December 1855—his father was Rector of the little village of West Harling, between Norwich and Bury St. Edmunds. He lost his mother when he was three—a disaster which may have been part-cause of the self-concentration in his character. When he was five the family moved to Cobham in Kent and remained there for some time. His earliest school was in the country near Tonbridge, and thence he joined his brother, Stuart, at Haileybury. Country sights and country sounds were his wherever he resided ; and with an intense urge to collect, what else could he collect but country objects. The priest of a parish near Cobham instilled into him ideas of system in collecting ; and when he reached Haileybury he had the guidance of a named collection of insects in the school museum. Stuart was collecting butterflies ; therefore he collected beetles. The school encouraged him in collecting by printing his "List of the Mammals and Coleoptera of Haileybury ".

The two boys left together, Stuart for Oxford, he for a tutor at Medmenham, on the Thames near Henley, where, the tutor having some biological knowledge, he was encouraged in Zoology. Following Stuart to Oxford—his college Exeter, his chief teachers the professors Sir Edwin Ray Lankester and George Rolleston—he obtained a biological degree in 1878. He had made the lightest of contacts with the Professor of Botany, Malmaduke Lawson, but an excellent contact with the Professor of Geology, Sir Joseph Prestwich. Next he obtained a Burdett-Coutts scholarship which gave him work in the Geological Museum and led to research on recent fossils from quarries near Oxford. Meanwhile he was seeking a museum post: this when it came was neither zoological nor geological ; he was taken into the Botanical department of the British Museum (Natural History) in the place of Henry Trimen who had become Director of the Botanic Garden at Peradeniya, Ceylon. In Trimen's shoes at the Museum it was his duty to study and to keep in order the collection of the Monocotyledons. Cause and effect combined : Monocotyledons remained his for life. His qualifications for the post which came to him so unexpectedly, were those of an excellently observant naturalist, a knowledge of the British flora, a training in taxonomic methods and an intense ardour. Settling in London, he obtained election to the Linnean Society in 1881 and took full advantage of its personal contacts and its library. Then he began to travel ; first to wander, botanizing, in Dorset, then in Kerry, next in the Shetlands, in the Alps and in Arctic Norway. The Royal Society sent him in 1887 along with a zoologist from Edinburgh, George Ramage, on a six weeks visit to the island of Fernando de Noronha in the tropical Atlantic at 194 miles from the Brazilian coast. Returning, he reported on his collections in a paper published by the Linnean Society.

In 1888 he was selected by the Colonial Office for the post—a new post—of Director of Gardens and Forests, Straits Settlements. The idea of an official botanist was too new for the colonists and he suffered as a pioneer their misunderstandings of his purposes. The model for his post was in Ceylon where, from long before 1888, there had been an officer having the care of the public gardens, with the furtherance of their amenities and their lessons, charged with supplying from them material for cultivation and required to influence the planting through offering the best ; and, thirdly, charged with bringing the Colony into the comity of international botany by investigating the flora. Ridley left for the East with instructions to call at Florence on the great naturalist, Odoardo Beccari, to get from him suggestions regarding travel, and to proceed to Peradeniya to learn what Trimen was doing

with his Para-rubber trees. He paid these visits and reached Singapore towards the end of the year.

He found himself, as regards the Botanic Garden, dealing with a committee whose control he resented as unconstructive ; for the other facets of his work he dealt direct with the Government. The Governor must have sided with him as opposed to the Committee, for he made him Chairman of it to strengthen his position. Though the Garden had had the name Botanic Garden for 29 years, it had only deserved it for 14 : from being park-like with coconut palms and local fruit-trees in plenty, with roads for riding and with a certain amount of flower beds, a trained horticulturist from Kew had converted it, introducing from 1874 selected exotics and the custom of naming what was displayed. This horticulturist was Henry J. Murton. When Murton after much energetic planting complained of lack of further space, he was allowed to expand into an adjoining " military reserve " and thither had gone in 1877 the Garden's first Para-rubber trees. Nathaniel Cantley, Murton's successor and Ridley's immediate predecessor, used the Military Reserve for raising shade-trees for the roads of the island. Ridley made the ground into an extensive nursery ; and it constituted a separate unit, the Economic Garden. When he arrived the Para-rubber plants in it were 9 twelve years old, 21 five years old and about 1000 seedlings—and this was the nucleus for the enquiry that he had been told to undertake. The word " Forests" in his title meant that the locating of valuable timber trees was a part of the study of the flora to which he was to pay close attention. A Zoological Section had been injected into the Garden in 1870. It dwindled and dwindled, but had not gone until 1904.

Ridley began to travel and explore at once. He visited Penang and Malacca; then the Governor took him up the East coast in his yacht. He was soon in Malacca again delimiting forests : and then he was attached to the annual survey of Christmas Island. In 1891 he visited the Thaiping hills and later in the year, with two companions attempted to reach Gunong Tahan, the highest mountain in the Peninsula, by boating up the Pahang River. The attempt failed ; it was something impossible at that time and the mountain was not climbed until 1905. In 1892 he accompanied D. F. A. Hervey, then Resident at Malacca, up Gunong Mering, a subsidiary of Mount Ophir. There was another visit to the Thaiping hills in the next year. He was making a set at the mountains.

Within a few months of taking up his appointment he became a member of the Straits branch of the Royal Asiatic Society and its Secretary. The branch had been founded by a group of scholars " for collecting and recording scientific information on the Malay Peninsula and Archipelago " and had done valuable service in languages, but scarcely more. From Ridley's adhesion until he retired in 1911 scarcely a year passed without a contribution from him to its Journal ; and the first of these made history. It was a " Report on the destruction of coconut palms by beetles " and the picture he gave caused the Government to pass a " Coconut trees preservation order " giving powers to him as Director of Gardens to see to its enforcement.

I return to the subject of rubber. When the first 9 seedlings were planted in Singapore, the same number were planted in the Residency grounds at Kuala Kangsar, Sir Hugh Low being the Resident in the State of Perak. When they were old enough, Low's successor was asked by Low from Britain to ascertain if they bled on tapping ; and in an unconsidered trial he failed. He returned to the subject at the time of Ridley's appointment in similar manner with the same result, ordering, it is said, at the end " the useless trees " to be cut down. Something saved them ; and they were actually the source of the first Malayan Para rubber marketed in London. The Resident's report, given out from Kuala Kangsar, was a direct challenge to Ridley's instructions

from Kew and he proved its falsity at once by exhibiting rubber prepared by him from the sister trees in Singapore. Ridley soon discovered in his tapping the value of reopening his cuts ; but it was left to Willis and Parkin in Ceylon to explain this physiological response to wounding. Ridley initiated experiments in curing rubber as well as in tapping.

Trouble blew up in 1894 out of the circumstance that the expenditure of the Colony was in excess of its revenue, and orders were out for retrenchment. Unfortunately for Ridley these came when he had finished his first period of service and had applied for leave, made urgently necessary by a severe attack of sprue. Before the Governor, appointed to effect the retrenchment, could arrive in Singapore the senior civil servant, administering from the outgoing of the last Governor, created a committee of himself, the head of the military establishment and the oldest of the Unofficial Members of the Legislative Council to find economies. All three had experience of the Colony when as yet it had no botanist and they decided on a return to that condition. Ridley's post was announced as abolished ; and he left for home under this cloud. But from Kew the abolition was immediately resisted by Sir William Thiselton-Dyer ; the officers of the Linnean Society had the luck of making a personal contact with the Secretary of State for the Colonies, and a cablegram went out to the effect that no proposal to dismiss Ridley would be entertained. It is undeniably true that the immediate prosperity of Malaya rested squarely on that momentous cablegram. It was not that Ridley held any secrets ; but that the Retrenchment Committee, apart from its ungenerousness, was blind to the circumstance that agricultural interests were listening to the advice that Ridley had been giving for six years. Ridley curtailed his leave and returned to Singapore whence he was deputed to Selangor, not in any connection with rubber, but to advise the Federated Malay States where in Selangor there were forests proper for reservation. This he did, and at the same time he drew up an account of the timbers, illustrated by a collection of samples in duplicate, one set for Singapore and one for Kew. It was his last official connection with forest management, and his title was reduced to Director of Gardens as the Peninsula put the charge of its forests into the hands of forest technicians.

Ceylon was ahead of Singapore in the matter of rubber and had been testing the London market, finding it favourable : and the most aware of the planters in Malaya knew this. Then a Malacca-born Chinese landowner, Tan Chay Yan, confident of a market, but uncertain what tree to use, covered 40 acres near the town of Malacca with a mixture of the Assam rubber fig and the Para-rubber tree (1897), and in 1898 a much larger area of land close under Mount Ophir with Para alone. His lead was so rapidly followed that—to the immense gain of the Government by sales of land—50,000 acres in ten years and 96,000 in fifteen were planted between the forests that Ridley had been demarcating in 1892 for reservation. In a happy allusion at the Ridley Centenary Celebration, 1955, Sir Richard Winstedt said that after Raffles Ridley held the first place for altering the appearance of the land.

Ridley had his overdue leave and, returning, found himself in great demand as an adviser to the new planters. He held also the chief source of the seeds that they needed, three million of which went to them during the next years from the trees that his prescience had provided. He had in his early service sought to reach the planter by occasional bulletins : from 1901 he worked these bulletins into a periodical, the *Agricultural Bulletin of the Straits and Federated Malay States*. It lasted under his editorship until 1911 as an outlet for the writing up of various crops. When he wrote up spices, the result being too large for the monthly, he published it as a book under the title *Spices*. It had a good press as holding all that the planter needed.

By 1900 he had become an authority on the flora of Malaysia and botanists

began to ask him to name up their collections. It gratified him to please them ; but by the side of the planting demands it made him too busy. Furthermore he had determined on writing a Flora of the Peninsula. The consequent compromise went against the background of collecting data for the Flora. When a planter asked for advice he might receive a reply in this manner :— " Monday is a public holiday ; I will give Sunday to your trees, if you will enable me to spend Monday collecting in your jungle ". He would be back in Singapore on Tuesday morning with his collecting apparatus gorged with wet plants ; and the Malay plant-collectors would be occupied all day and possibly more than the day at fires in the office basement drying the specimens while he was getting through the office work above, too impatient to delay until they had done all, but had whatever became dry enough submitted for annotation as it was ready. Not seldom the bits of the one species would get two numbers because they came to him at different times. This might have led to less misunderstanding were it not that it removed slow-drying fruits from flowers and that, if later he detected the misnumbering, he would not find time for altering the numbers. Asked why he did not number in the field, he replied " there was no time ". There was also no time to make sure that the memorized field observations always reached the right specimen.

The Flora, when he came to the writing of it suffered from the same consequences of haste. His output of print in the last ten years of service in Singapore was extremely large ; his energy tremendous. In the last of these years he rushed up to Peninsular Siam to determine how far north the Flora was to extend and came back having decided on 7° N. He went north again on a hurried visit to Saigon and Angkor Wat for a hasty impression of the vegetation. He climbed Gunong Tahan, the mountain that had defeated him in 1891. Then he sailed for home and domiciled himself at Kew with the writing of the Flora his immediate purpose. He had left behind him a Botanic Garden of beautiful trees. As most of the exotics had been less than 14 years old when he arrived in 1888, it had needed steady faith in his mission to bring them so perfectly to maturity. Such service for the Public, though always likely to go unrecorded because amenities are not directly measurable, is great, and certainly was in his case. The other commissions of 1888, innate to his post, had been carried through with success and it must be said with genius. The *Flora* was not of them, but a project of his own. He seems to have invited no co-operation though he could have had it. In this as in general he walked alone.

He had resolved to avoid the British winter by travel ; and his recurrent absences from Kew had the same effect on his work as the absences from Singapore had had. The five volumes of the *Flora*—2936 pages—appeared in succession from 1922 to 1925. When it was off his hands he devoted his time to writing his *Dispersal of Plants throughout the World*, a naturalist's book of 764 pages, full of data that stir the reader to thought. It appeared in 1930.

Late in life he married Lily Eliza Doran, and grew old under her intense devotion. He died seven weeks short of the age of 101 on 24 October 1956, in the house at Kew which he had bought in 1912. His chief honours were election to the Royal Society in 1907 ; appointment as a Companion in the Order of St. Michael and St George in 1911 ; the Rubber Plantation Association's gold medal in 1914, the Frank Meyer medal for plant-introduction of the American Genetic Association in 1928 ; the Linnean Society's Linnean medal in 1950 and the Colwyn medal of the Institute of the Rubber Industry in 1955. There is a long list of other awards and honours in the pages of *Who's Who*.

I. H. Burkill.

Geoffrey Howorth Spencer Wood, M.A. (Oxon.), F.L.S., Forest Botanist, North Borneo, died in hospital at Kuala Belait on 5 May 1957 as a result

of burns sustained in an accident at his camp whilst on a collecting tour in Brunei.

He was the only son of Arthur Seward and Honora Penelope Wood of Whitehouse, Vowchurch, Herefordshire. He was born 12 August 1927 and was educated at Aymestrey School, near Worcester, and Clayesmore. He gained the Milligan Open Scholarship in Natural Science to Keble College Oxford in 1945, where he read the Honour School of Botany. He graduated with 2nd Class Honours in 1948 and also won the Colonial Probationership for Forestry. After studying Forestry for a year he proceeded on his first tour in Uganda but returned to Oxford to take the Final Honour School of Forestry in which he was awarded 1st Class Honours in 1952. On returning to Uganda he was appointed D.F.O. for the Province of Busoga but transferred to the Colonial Research Service as a Senior Scientific Officer to take up the appointment of Forest Botanist to North Borneo. After a few months' study at the Forest Research Institute at Kepong, Malaya, he reached North Borneo in 1954 where his programme included special investigations into species of the Dipterocarpaceae. He made representative collections from widely separated areas which involved lengthy tours into the little known interior : efforts were intensified during the exceptionally prolific Dipterocarp flowering season of 1955. His collections of preserved material greatly enriched many herbaria including those at Kepong, Kew, Leiden and Oxford. On his first home leave from North Borneo he was granted three months extension to study these specimens. He showed an appreciation of the applied aspects of his work and arranged for sample logs to be sent to the Forest Products Research Laboratory, Princes Risborough, for full-scale testing. The tragic accident occurred only two months after the start of his second tour. It is to be hoped that this promising work on the systematic descriptions of the Dipterocarps of Borneo, an area particularly rich in species of this family, will be suspended only temporarily, especially in view of the greater exploitation of the timber resources of south-east Asia since the Second World War.

He collected Bryophytes in East Africa and North Borneo : several of these specimens have been described and some new species named after him.*

His publications included :—

(1) Wood, G. H. S. & Chenery, E. M. (1955). Regeneration of *Chlorophora excelsa* (mvule) in Uganda in relation to soil-root conditions. *E. Afr. agric. J.*, **21** (1) : 34–41.

(2) Wood, G. H. S. (1955). The Dipterocarp flowering season in North Borneo, 1955. *Malay. For.*, **19** (4) : 193–201.

(3) Wood, G. H. S. & Agama, J. (1956.) *North Borneo Forest Records No.* 6 *Check List of the Forest Flora of North Borneo.* Sandakan.

(4) Francis, E. C. & Wood, G. H. S. (1955). Classification of vegetation in North Borneo from aerial photographs. *Malay For.*, **18** (1) : 38–44.

He was a proficient mountaineer and had climbed the main peaks in the Ruwenzori Range and Mts. Elgon, Kadam and Kilimanjaro in East Africa, Mt. Kinabalu in North Borneo as well as in the Alps and British Isles. He combined this recreation with a special interest in the ecological sequence of mountain flora. He was an enthusiastic photographer and made an extensive collection of botanical subjects. He enjoyed travel and made full use of his local leaves to tour in the Belgian Congo, Kenya, Tanganyika and Malaya, in the Himalayan foothills and in Hong Kong. He delighted in the sailing of small craft both on Lake Victoria Nyanza and in the estuaries of North Borneo

* Potier de la Varde, R. (1956). Contribution à la flore bryologique africaine (8e article), *Rev. Bryol. Lichènol.*, **25** (3–4) : 213–233.

and Brunei and played most games with enthusiasm. When an undergraduate he flew with the Oxford University Auxiliary Air Squadron.

J. D. Bletchly.

Arthur Mayfield, elected F.L.S. in 1921, died at Mendlesham, Suffolk, on 5 September 1956, in his 88th year. Born in Norwich, he developed an interest in natural history early in life and was in the habit of visiting the Norwich Museum as a boy, there receiving encouragement from the then curator, James Reeve. Becoming a teacher, he held posts at Norwich and Great Yarmouth between 1883 and 1896, when he was appointed head master of Mendlesham village school, where he continued to work until retirement in 1931.

Joining the Norfolk and Norwich Naturalists' Society in 1893, he soon contributed papers on Norfolk earthworms and mollusca to its *Transactions*. He was made an honorary member of the society in 1945. Within a few years of taking up residence in Suffolk, he had become the leading authority on that county's bryophytes, lichens, fungi, mycetozoa and mollusca and in due course he contributed numerous papers on these groups, mainly in the form of annotated county lists to journals published by the Ipswich and District Natural History Society, the Ipswich and District Field Club, the Suffolk Naturalists' Society and the *Journal of Botany*. His integrity and critical faculties were of the highest order, so that his published records may be relied upon for their accuracy. He presented his collections of bryophytes, lichens and mycetozoa to Norwich Castle Museum shortly before his death, but his extensive herbarium of micro-fungi was rendered useless through infestation by psocids in his house and was destroyed by him with the exception of a few specimens which he passed on to the Commonwealth Mycological Institute at Kew.

He was a greatly beloved and respected school master and took an active part in village affairs. A man of varied interests, he was one of the small group of enthusiasts who supported W. G. Clarke in founding the Prehistoric Society of East Anglia (now the Prehistoric Society). He was organist and choirmaster of St. Mary's Church, Mendlesham, for twenty-five years. His wife, two sons and a daughter survive him.

E. A. Ellis.

JOINT DISCUSSION WITH THE SYSTEMATICS ASSOCIATION ON " THE INHERITANCE OF ACQUIRED CHARACTERS "*

Opening Address. By H. Graham Cannon.

The real interest in the so-called problem of the inheritance of acquired characters is as to whether or not it forms a possible evolutionary mechanism. Naturally a definition of what exactly is meant by an " acquired character " is essential. In the early twenties in *Nature* there was an absurd discussion which centred round a letter which maintained that since all forms develop from an egg clearly all characters must be " acquired " during development ! Now this statement is wrong from two aspects. First, " acquired character " is a term of two words which have obtained a particular meaning which is well known to the biologists who use the term, so there is no need to squabble about it. But secondly, is it right to say that all characters are acquired by an organism during its development ? Is there not one which is *not* acquired, which is not even inherited, but rather is *inherent* in the egg itself ? I refer to the character, the ability of the protoplasm of the egg to produce more protoplasm of the particular kind specific to that egg. Surely that is a character of an organism, and moreover one of its most essential characters. I think that at the end of my talk I shall be able to show more emphatically the significance of this point.

Now as to the actual definition of the term, I quote from Leonard Doncaster, a most meticulous worker, who defines it as " A feature developed during the life of the individual possessing it, in response to the action of use or environment ". Then he states that " *as a rule* " such acquired characters are adaptive, that is, they render the organism or structure better fitted to its surroundings than if they had not been developed—but *not always*. Now I think this ambiguity in the definition has been responsible for so much of the trouble that has arisen over the numerous attempts at experiment to prove or disprove the inheritance of acquired characters. And I am afraid it has to be admitted that most of the experiments were carried out with a preconceived idea as to the results to be obtained, and for this reason alone they have been viewed askance.

There have been two distinct types of experiment, depending on whether the change in the environment which produced the acquired character was normal or abnormal, and as a result there have been produced two distinct types of acquired character. Thus the character which Kammerer purported to have dealt with was normal. He said that he caused the midwife toad, *Alytes*, which normally breeds on land, to breed in water. This, he said, caused the *Alytes* to produce the horny thumb pads that are characteristic of those Anura which breed in water. This was the acquired character. Of course we know now that the whole thing was a fraud, but the idea was right. The change from breeding on land to being forced to breed in water is one which might easily occur normally. No, Kammerer had the right idea scientifically but the wrong idea morally. And then take MacBride's last experiments on the stick insect. He taught these insects, by depriving them of their normal food, privet, to feed on a substitute, ivy. Again this is a sort of change which might easily occur in nature when one source of food supply becomes scarce. Now in both these cases as might be expected the acquired character was an adaptation.

But now, compare these types of experimental acquired characters with some that have been produced or attempted. There is, of course, the absurd case of cutting off the tails of mice for generation after generation and seeing what the effect would be. But the most fantastic case I can remember was told to Bateson by Goldschmidt. They were discussing Guyer & Smith's

* See *Nature, Lond.* (1956), **178,** 1210, for further account.

experiments on inherited eye defects. Goldschmidt said that a German had shown that if solid naphthalene was injected into the stomach of pregnant rabbits, the young were born with eye defects. Why anyone should want to carry out such a revolting and absurd experiment passes my understanding. But it illustrates my point that this acquired character is produced in the individual—the foetal rabbit—by an absolutely abnormal change in its environment, that is, one that could never have occurred naturally.

But now it may be argued that there is no real significance between what I have called these normal and abnormal experiments. In fact, it seems to me that the modern geneticist *must* argue in this manner. For surely according to the Neo Mendelian "the characters which an animal or plant inherits are controlled by a series of separate . . . units known as genes" (*Waddington* 1952, *Third Programme*). That is, *all* the characters of an organism. There can be no exceptions or the whole fabric of Neo Mendelism *as an evolutionary mechanism* falls to the ground. No, to the Neo Mendelian all characters and therefore all acquired characters if they *are* inherited must be the same genetically. However what puzzles me most is why modern geneticists worry their heads over this stupid problem. After all, the Mendelian Theory or rather I should say, the Neo-Mendelian Hypothesis allows for all eventualities and therefore why not for the inheritance of acquired characters ? As Carter said "It is easy to imagine a gene doing anything we want it to do". No, as far as I can see, the inheritance or not of acquired characters cannot hold out any intriguing interest to the modern Mendelian. His hypothesis is all embracing—then let him take to his bosom what he erroneously calls Lamarckism.

Now as regards experimental analysis of the problem. The experiments are all of the same pattern : an animal is transferred from its normal surroundings to a strange environment to see if a new character (an acquired character) will turn up. It it does, in such a way that the characters can be seen and measured, the experiment may proceed. But here is the difficulty : the trouble is to force an organism to change obviously. Of course, every organism being in equilibrium with its environment *must* change somehow if external conditions change. But organisms, especially higher forms, are so full of homeostatic systems that they resist any change. In the lower forms there is not this degree of homeostasis and here it is relatively easy to produce a change which is obvious. However, once an acquired character has been firmly established, the animal is transferred back to the original environment and breeding is continued to see whether the induced character persists in subsequent generations. If it did, then said the experimenters, the inheritance of acquired characters has been upheld. But surely what it could show much more definitely would be that the environment had little effect on the animal, and this was the last thing that the so-called Lamarkians wanted to show. The whole experimental technique was unsound for "if a change from one environment to another causes a change in structure in one generation, a change in the opposite direction should be sufficient to reverse it in an equal amount of time". Now that quotation is from MacBride of all people, just a few years before he was up to the eyes in the whole sorry business. It is undoubtedly correct, but only as regards adaptive acquired characters. If however, the acquired character is induced by some abnormal circumstance it will be simply an induced mutation and therefore inherited in the normal Mendelian manner. It seems to me, therefore, that any attempts *experimentally* to demonstrate the inheritance of acquired characters are just so much waste of time.

Now as to my own views on the problem itself. A year ago I lectured here to the Linnean Society and one of the main points that I made was that to refer to a belief in the inheritance of acquired characters as Lamarckism is just nonsense for it is based on an ignorance of Lamarck's views. Lamarck enun-

ciated his views finally in 1809 (just fifty years before the *Origin*) as four laws, and it is in the fourth law that it is explicitly stated that acquired characters are inherited. But then I showed that this fourth law is actually redundant as it is covered by his second and third laws. His third law states that an organ develops proportionately as it is used while his second law states that an organ appears proportionately as it is required. Or, put another way, during the lifetime of an individual an organ and its related structures develops proportionately as it is used. During the continuance of a race, an organ and its related structure evolves proportionately as it is required. To Lamarck it is not a question of a new character appearing in one generation *and being handed on* to the next, because that character will appear in the next generation in any case because it is required (that is, according to his second law).

In this sense I am a true Lamarckian and so really the question of the inheritance of acquired characters does not interest me because it does not arise. I believe with Lamarck that if, as a result of changing environment, a new character, a new structure or habit, is required, then it will appear. Last year I gave examples showing that all the major advances in evolution illustrate this point. But what led me to this view was frankly the unsatisfactory nature of the modern Neo Mendelian mechanism with its complete reliance on the action of chance. As Waddington broadcast " the present theory bases itself essentially on the idea that new hereditary changes occur spontaneously and at random : that is to say they are not guided so as to fit the environment " ; or as Samuel Butler put it, evolution is considered as the result of " blind chance, working nowhither and due but to the accumulation of innumerable lucky accidents ". I cannot, as a functional morphologist with, I feel entitled to say, some real experience of what adaptations mean, accept this reliance on pure chance. As Paley said, " Universal experience is against it ".

You may say, this is merely a matter of opinion which will never be settled by argument. But there is another aspect where I feel that biologists as a whole are entitled to an answer from the Neo Mendelians. I maintain that, whatever view one takes of the Neo Mendelian Hypothesis, this mechanism can be carried back *only* as far as the first Metazoa (the first cellular organism) but *no further*. My reason for believing this is that the proof of Mendelian Inheritance, and it is as sound a proof probably as exists in the scientific world, depends at each step on chromosomes. and moreover, not merely on the *existence* of chromosomes but on their orderly behaviour. You cannot have genes without chromosomes, for unless a particular gene occupies a particular place on a particular chromosome, it cannot produce its own particular effect. Moreover it is bound to behave in a certain way during meiosis. Any divergence leads to disaster. An unruly gene is a contradiction of terms. Now chromosomes did not appear in evolution until the appearance of the cellular structure in the organism and sexual reproduction. I am well aware that in the Protista there are *simulacra* of both chromosomes and sexual reproduction, but the point I want to make is that the details of mitosis and meiosis on which the proof of the Mendelian law is based appear suddenly at the origin of cellular organisms, and have come through to the present day practically unchanged. During the Protistan Age I imagine that a variety of reactions took place between individuals which have come down to the present day as what we know as conjugation. But this is not sexual reproduction. Only along one line, the line that led to the cellular organisms did this reaction persist as that sexual process. Hence from the first cellular forms up to modern forms there is the possibility of Mendelian Inheritance.

But if we go back further to the bacterial level, surely everybody must admit that there are no nuclei and there is no sex, that is, nuclei and sexual reproduction of the strictly orthodox type that occurs in all Metazoa. How

then can there be Mendelian Inheritance? How any biologist can talk of genes in any organism that does not show cellular differentiation passes my understanding. But suppose we go back further, to the virus level where there are not only no cells but no individuals. Now in these early forms—what I call amorphous types—there must have been an inheritance, for without inheritance there could not have been any continuity of type. Let us think what these earliest types of living matter must have been. We do not think nowadays—as did the Victorians—of something like *Amoeba* as the primordial type. We think rather of an amorphous protoplasm, a primordial slime, a collection of chemicals in equilibrium with its environment, that had the characteristic property of being able to produce more protoplasm of its own particular kind. That was the property which distinguished protoplasm as a living material from any other chemical mixture in equilibrium which did not have this property and hence was non-living.

Now when I use the word "equilibrium" I do not use it in the strict physico-chemical sense with closed systems. I mean that the particular chemical mixture persists in time with sufficient constancy for us to talk about its characteristics. I know this is not a very accurate description, but if I say simply *dynamic* equilibrium with its environment, I think every biologist will understand what I mean. Now amorphous protoplasm was a chemical mixture in equilibrium with its surroundings and, like any other system in equilibrium, it must have reacted to any change in its surroundings. But it must have reacted in a particular way and that is according to the physico-chemical law of Le Chatelier. Now according to this law it would always react in such a way as to re-establish equilibrium. In other words, it would always do the right thing *to bring about its own continued existence*; or, put another way, if a change in the environment demanded—for continued existence—a particular new change or character, then whether or not that character was physiological or morphological that new change or character *must* have appeared, in other words, Lamarck's second law.

Now this is the state of affairs that must have obtained during all that time —how many aeons we do not know—between the first appearance of life on this earth through, first of all, the breaking up of the primordial protoplasm into units or individuals. This itself must have been, of course, one of the reactions of the primordial mass of living material to external change, probably a surface-volume relationship. Later, I imagine that a special arrangement of molecules within those individuals would be called for by the environment. This would be the first structural modification and once this started there is no end to where it will lead. But ultimately it led to the establishment of cellular constitution and sexual reproduction. Through all this time the property inherent in protoplasm of being able to adjust itself in the optimum manner to changes in its surroundings must have guided evolution.

Now when cells appeared, with their nuclei, chromosomes, sex and genes, what right have we to say that this inherent quality disappeared or even took a back seat? To suggest such a thing is to me wholly illogical. I maintain that this homeostatic property of protoplasm has continued with us up to the present day. It is W. B. Cannon's Homeostasis which he applied only to the physiological side of the organism but which I maintain *must* have applied to the morphological as well. It is the main motive force of evolution: it is the "harmonious control" which Waddington has had to call in to his assistance. As I see it therefore in any organism heredity is controlled in two ways. First there is that inherent quality of protoplasm which ensures that the organism always reacts in the optimum way in response to its environment. This I call organismal inheritance for it is the organism acting as a whole and clearly all changes brought about in this manner are functional adaptations. Secondly

there is that Mendelian mechanism which evolved so much later which deals with the inheritance of changes in structures or habits *once they had evolved*. These changes are purely random changes but, of course, if by chance any change turns up of selective value, that change will be selected by Natural Selection and perpetuated.

In view of this then, what is my attitude to the inheritance of Acquired Characters ? Clearly it depends on the character. If it is a necessity stimulated by a changed environment, then just as it appeared as a natural response, so it will continue to appear just so long as the environment demands. If, on the other hand, the acquired character is an induced mutation, then of course it will be inherited in the normal Mendelian manner. In both cases it can be claimed that there is the inheritance of acquired characters but what value there is in lumping together these two totally different genetical phenomena under one comprehensive term I fail to see. What I suggest is that the sooner we stop talking about the matter in these terms, the better it will be for all of us.

Automatic Adjustments in Bacterial Populations in Response to Environmental Changes. By A. C. R. Dean, Physical Chemistry Laboratory, Oxford.

Many strains of bacteria are very non-exacting in their growth requirements. For example coliform organisms can usually synthesize all the proteins, amino acids, polysaccharides and other substances necessary for their re-duplication from simple substances such as a source of carbon e.g. a sugar or certain carboxylic acids, together with ammonium and magnesium sulphates and phosphate buffer. This building up of complex products must involve long sequences of reactions and it seems therefore quite reasonable to postulate that in the growing cell a series of enzyme-like substances co-exist in a system and are linked in such a way that each one provides some kind of intermediate required for the building up of another. Indeed thermodynamic considerations make the linking of reactions a necessity in the growing cell since many of these reactions would result in a decrease of entropy if they were not compensated by others involving an even greater increase. In such a system a steady state is attained (after a period of irregular growth) in which each component increases with time in accordance with the autosynthetic law :

$$\frac{dX}{dT} = kX$$

and thus although an enzyme, protein or nucleic acid is not autosynthetic in isolation it does, when part of a linked series, obey the law :

$$\text{enzyme} + \text{metabolite (1)} = \text{more enzyme} + \text{metabolite (2)}$$

The importance of these considerations is that growth and function are closely linked and that when growth has been long continued in a given medium a stable proportion of the various components will be established and the proportions will be those which result in the optimum rate of growth in the given environment. When the conditions are changed these stable proportions will be upset but will eventually settle down to a new equilibrium. In the initial stages of the adjustment there are often irregular variations. These propositions have been examined in detail mathematically by the use of suitable models. I do not intend to discuss this mathematical treatment here but would refer you to the published papers of C. N. Hinshelwood *et al.* (Dean & Hinshel-

wood, 1955*a* ; Hinshelwood, 1946, 1952, 1953*a*, *b*). For the present it is sufficient to say that the models show in a very satisfactory way, to the physical chemist at least, how adaptive changes in bacterial populations could take place. A typical example will illustrate this point.

When *Bact. lactis aerogenes* which has been growing for some time in a medium containing glucose as sole source of carbon is first transferred to a medium with D-arabinose as the sole carbon source there is a lag of several days before growth begins and when growth does begin the rate is slow. Once this lag phase is overcome, however, it does not reappear on subsequent subculture although many subcultures may be necessary before the growth rate has reached its optimum value. The kinetic theory just described would postulate that in the glucose medium, since growth has been taking place for some time in it, the enzyme systems in the bacteria will be present in those proportions compatible with optimum rate of growth in that medium. On transfer to D-arabinose medium, however, enzyme systems which were not utilized during growth in glucose will be necessary and the time taken for expansion of these systems accounts for the lag phase. Considerable growth in the new medium will be necessary before the proportions settle down again to a new stable value and hence the growth rate will only reach its optimum value after some time in the new medium.

Another explanation is, however, possible, in that the lag phase may simply represent the time taken for a small proportion of spontaneously-occurring mutants in the inoculum to multiply. These alternatives apply when bacteria are introduced to new sources of nutrient in which they are reluctant to grow, and also when drugs are added to the culture medium. To decide which mechanism operates it is necessary to examine each example separately and to determine the proportion of organisms taking part in the response. I propose to discuss now a few of the examples which have interested us in Oxford and in which we think that mutations are not involved. For other examples the reader is referred to Dean & Hinshelwood, 1955*a* and Hinshelwood, 1946.

The example of *Bact. lactis aerogenes* and D-arabinose has been referred to already. Another line of evidence arises from the fact that towards the end of the lag phase there is a considerable increase in cell mass before the cell number increases (about 40 per cent), and therefore the majority of the cells are participating in the adaptive response (Baskett & Hinshelwood, 1951). Similar results have been obtained with *E. coli* in sucrose and with a yeast strain in galactose (Mims & Hinshelwood, 1953 ; Kilkenny & Hinshelwood, 1952).

Further evidence in support of the non-genetic nature of the response of *Bact. lactis aerogenes* to D-arabinose arises from the finding that when cultures just starting to grow on D-arabinose were plated out on glucose agar and single colonies isolated and tested no stably adapted strains of bacteria were obtained, all undergoing rapid reversion. Moreover when in the early stages of adaptation sufficient glucose was added to support 2–3 cell divisions a considerable loss of adaptation occurred. Under these conditions the selection of reverse mutants or of untrained cells could not be important (Hinshelwood & Jackson, 1950 ; Baskett & Hinshelwood, 1952).

The example of *Bact. coli mutabile* and lactose is also interesting (Dean & Hinshelwood, 1954*b*). As in the previous example there is a lag of several days in liquid media. When plated on solid media containing lactose as the sole carbon source the response varies with the size of the inoculum. For example, when 10^8–10^9 cells are plated about 200–300 large colonies are formed within 3–4 days. On the mutation theory these would represent the pre-existing lactose-utilizing mutants in the inoculum. When about 100 cells are plated they all form large colonies although they may take longer to do so than when

10^9 cells are plated. This would indicate that all the cells in the culture are capable of utilizing lactose. One explanation which has been given for this apparent paradox is that the media used in bacteriological experiments contain traces of unavoidable impurities sufficient to support a population of about 10^8 cells so that on the low-inoculum plates each micro-colony (resulting from growth on the impurity) would be certain to contain at least one lac + (lactose-utilizing) mutant (Ryan, 1952). Although micro-colony formation does undoubtedly take place a further experiment invalidates this latter explanation. It involves the withdrawing of samples at intervals from a culture lagging in liquid lactose medium. When these samples are diluted and about 100 cells plated on lactose agar it is found that the longer the sojourn of the cells in the liquid medium the shorter is the plate lag, thus showing that the bulk of the population are undergoing an adaptive response. For if on the one hand growth on the plates depends on lac + (lactose-utilizing) mutants arising in the micro-colonies the time of appearance of the lac + colonies would be constant and would bear no relation to the time passed previously in the liquid medium. If on the other hand spontaneous lac + mutants are selected during the sojourn in the liquid medium, the number of colonies on the plates should steadily increase as the lag progresses. This is not so (Dean & Hinshelwood, 1954*b*). This latter type of experiment has also been carried out successfully with *Bact. lactis aerogenes* and D-arabinose (Baskett & Hinshelwood, 1952).

With regard to the early arising colonies on the high-inoculum plates, we find that although the colonies may arise earlier than when 100 cells are plated they nevertheless take longer to reach a standard size than fully adapted cells do, and thus lac + mutants could not have been present from the start unless it is assumed that their growth is inhibited by the large excess of lac − (lactose-non-utilizing) cells in the inoculum. Direct experiments shows that this does not happen (Dean & Hinshelwood, 1954*b*). In fact it has been shown on purely statistical grounds that when massive inocula are plated a small proportion would be expected to develop earlier than the majority. By their development they would exhaust the medium and thus prevent other cells from developing into large colonies. The conclusion that such early arising colonies are derived from special mutant cells in the large inoculum is thus unjustified (Dean & Hinshelwood, 1956).

The behaviour of bacteria when introduced into drug media is also capable of interpretation by a kinetic point of view. At suitable concentrations of drug there is usually a lag phase which has to be traversed before growth begins, and so the mutation-selection theory is again a possible explanation. The lag does not usually reappear on subsequent subculture at the same drug concentration and in many cases it is possible, by gradually increasing the drug concentration, to obtain strains of bacteria which will grow in concentrations of drugs many times greater than that which would have been lethal if the cells had been introduced directly into it. Sometimes the resistance is continuously graded to conform to the concentration at which the cells have been trained. A good example of this is found with *Bact. lactis aerogenes* and proflavine and is easily explicable by the sort of automatic adjustment already described (Dean, 1955). The alternative is to assume a complex polygenic system, a theory which encounters further difficulties when the behaviour on solid media is considered. For example when colonies are picked from proflavine plates and re-tested for resistance, it is found that resistance or non-resistance on re-test depends on the buffering capacity of the original drug medium (Dean & Hinshelwood, 1955*b*). Proflavine is antagonized by the acids produced by the growing cell and hence if the medium is lightly buffered the cells which have become trained to proflavine will de-train again once the acid has antagonized the drug. If the medium is well buffered no de-training will take place.

Additional and improbable genetic assumptions are required to explain these findings and the picture becomes even more complicated when one considers that during the course of the training in liquid proflavine media violent fluctuations in growth rate occur between one subculture and the next, a finding which would necessitate the assumption that at one stage slower growing mutants are selected in preference to faster growing ones (Dean, 1955 ; Dean & Hinshelwood, 1954*a*).

When the resistance to drugs is not graded, but there is a sudden jump to almost full resistance, this does not necessarily mean that a fully resistant mutant has been selected out. A physico-chemical explanation would be that the cells are saturated with the drug when the concentration in the medium is relatively low. Obviously, here again, direct investigation of specific examples is necessary. Further results which are incompatible with the view that the cells forming colonies on drug plates exist in the inoculum as fully adapted resistant mutants were obtained when trained and untrained cells of *Bact. lactis aerogenes* were plated on solid media containing brilliant green, proflavine, streptomycin (concentrations above 30 μg. per ml.) and terramycin. It was found that those few cells from a large inoculum of untrained cells which succeeded in forming colonies at all took a longer time to do so than did previously trained cells, indicating that a considerable amount of adaptation takes place on the plates. Similar results were obtained with *Bact. coli mutabile* and chloramphenicol or propamidine. Moreover the conclusion that, when large inocula are plated and few cells survive to form colonies these colonies necessarily arise from spontaneous fully resistant mutants in the inoculum, is just as open to criticism on statistical grounds as in the example mentioned earlier when the adaptation to carbon sources was discussed (Dean & Hinshelwood, 1955*b*).

I have attempted to show how adaptations in bacteria may take place by a kind of automatic adjustment in response to the environment. While it has been admitted that a considerable degree of adaptation in bacteria is possible, many workers are reluctant to admit that stable heritable changes can take place without genetic mutation, since this they say would involve the inheritance of acquired characteristics. The changes which I have just described are heritable insofar as they are passed on to succeeding generations. But it is surely to be expected that in cells which reproduce by binary fission the progeny should have the characteristics of the parents. This is quite different from higher forms where special germ cells are set aside for reproduction. The strains mentioned in this paper do not undergo recombination.

Are these changes ever stable ? It is our experience that an adaptation which has been lightly impressed on bacterial cells is easily lost when the cells are returned to the original medium. The longer the training is impressed the more permanent does it become until eventually it appears to be stable. But the stability is never absolute although it might appear to be so to an ordinary sort of test. For example, we have subcultured *Bact. lactis aerogenes* in proflavine, propamidine and chloramphenicol media until more than 1000 generations had elapsed. During the first 300–600 generations in drug-free medium, the number depending on the experiment in question, the strains appeared to be reasonably stable ; but on continued subculture they eventually lost their training, and in a manner which did not suggest the emergence of reverse mutants. So what appeared at first sight to be stability was merely sluggishness of reversion for which good physico-chemical explanations can be given (Dean & Hinshelwood, 1954*a*).

Are the changes acquired ? It is our argument that these experiments involve the development of existing enzyme systems rather than the acquisition of new ones.

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Possible Mechanisms for the Inheritance of Acquired Characters.

By R. Melville.

(With one Text-figure.)

The possibility of the inheritance of acquired characters has been hotly debated ever since the days of Lamarck, but it is only within the last decade, that any considerable body of experimental evidence has been produced in its support, of a kind that could be sustained by chemical and physical arguments, in addition to the biological probabilities. Much of this evidence concerns unicellular organisms such as bacteria and yeasts and some of the most convincing comes from Hinshelwood and his co-workers.

The general nature of their results is as follows. The organism is transferred from the culture medium on which it is accustomed to grow, to one in which its normal source of carbon or nitrogen is replaced by a different compound. Alternatively, some toxic substance is added to the medium in sub-lethal concentration. In either set of conditions, the organism is unable to grow for some time—this is the lag period—and then starts to grow and continues thereafter to grow normally. After a variable period of normal growth on the new medium, the organism becomes so adapted to it, that it is unable to grow on the original medium, without a period of readaptation. Before the readaptation is complete, however, transfer to the original medium results in immediate growth, with loss of adaptation to the new medium.

Two theories have been advanced to account for these observations. The *Mutant Theory* postulates, that in the normal course of cell division, there is always a small proportion of mutant individuals arising spontaneously, which possess distinct new heritable characteristics. It is supposed that suitable mutants grow on the new medium offered to them.

The *Adaptation Theory* postulates that in the new environment there may be either an expansion of existing enzyme systems to deal with the alternative food substrate, or existing alternative metabolic routes are exploited. In either case, time is required for the necessary readjustments and this accounts for the lag phase.

In response to criticisms, Baskett & Hinshelwood (1) carried out a series of experiments designed to test the alternative theories. The test organism was *Bacillus lactis aerogenes*, which grows normally in media containing glucose as a source of carbohydrate, and which can be trained to utilize d-arabinose as a substitute. The results made it clear that the presence of mutated cells could not explain the observations, but they were consistent with adaptation to the new medium having taken place in all or the majority of the cells. Among the more important points emerging were the following :—

1. When cultures are just starting to grow on d-arabinose, no stable d-arabinose-adapted cells can be isolated by plating single cells on glucose agar. Formation of colonies with glucose as the carbon source at this stage, results in complete reversal.

2. At the end of the long lag phase in d-arabinose, the bacterial mass shows a marked increase of about 40 per cent, before the number of cells shows any marked change. For multiplication of special mutants, the increase in mass would have to wait an approximately equal increase in numbers, so that the population as a whole must be adapting.

3. Co-operative production of intermediates by the cells plays an important part in the early stages of adaptation. Lag phases are appreciably shortened by increasing the concentration of cells, or by the addition of sterile filtrate from fully grown d-arabinose cultures. When very dilute inocula are used, the lag period becomes very long—up to 3 weeks or more.

There is, then, considerable evidence that unicellular organisms can adapt themselves to new conditions and, that after a time, the adaptations are inherited. The situation is much more complex in a multicellular organism. Phenotypic responses to changes in the environment are not inherited. Not infrequently they affect organs remote from the germ cells and there seems no reason why such temporary changes should be inherited. Moreover, it would be disadvantageous to a long-lived organism if short-term environmental adaptations were at once inherited. In such circumstances, the organism might have to change from year to year, or even more frequently if there were several generations in a year. The stability of the genetical system effectively prevents the inheritance of temporary phenotypic adaptations.

An organism may be permanently placed in an altered environment by dispersal, or by other means, or it may be subjected to a slowly changing environment by climatic drift, soil erosion or other edaphic changes. In such circumstances, there may be a relentless pressure to adapt and failure to do so may mean extinction. That adaption takes place in response to environmental changes seems evident from orthogenetic evolution, for example in horses and elephants. There are many special adaptations, also, that appear to be responses to the environment. The questions are, how does adaptation take place and how does the controlling mechanism become fixed in the genetical system of the nucleus ? I believe tentative answers can now be given to these questions.

The initial changes in adaptation are probably of a similar nature in unicellular and multicellular organisms. They depend upon the exploitation of existing enzyme systems or of already existing alternative metabolic routes as suggested by Hinshelwood. The unicellular organism passes through a lag phase, during which it readjusts its metabolic processes and after a while it settles down into a new metabolic rhythm. The new metabolic state in the multicellular organism is a temporary one and results only in a phenotypic response. Nothing more can happen and nothing more does happen, unless the environmental pressure is maintained for a number of generations. Then, the constant association of the particular train of metabolic events results sooner

or later in an essential molecule or molecules becoming attached to a protein molecule. The protein may be ribose-nucleic acid contained in a cytoplasmic granule. The adaptive metabolic system is now tied to a particle. It will probably have the properties of a plasmagene and will be transmitted from cell to cell. It may now pass into the germ cells and may be carried over, more or less sporadically during fertilization. At this stage, the threshold of inheritance has been reached. Subsequent events in the incorporation of the new mechanism controlling the adaptive character into the hereditary genetic system follow the scheme set forth by Darlington & Mather in their *Elements of Genetics* (2). The plasmagene becomes attached to a gene and is incorporated into the nucleus. The whole process is summarized diagrammatically in fig. 1.

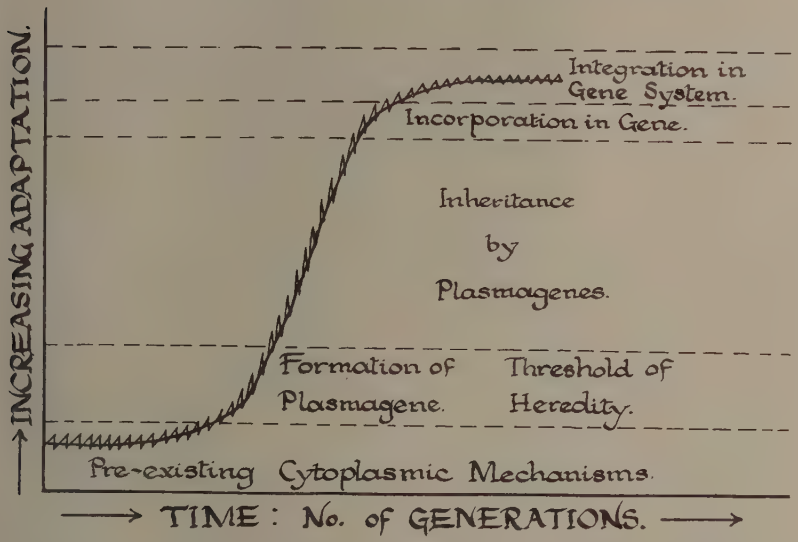

FIG. 1.—The fixation and inheritance of acquired characters. The continuous curve indicates the probable trend of adaptive mechanisms with time. The broken curve indicates the fluctuations of effective concentrations of key metabolites with each successive generation. Adaptation passes through a non-heritable phase of phenotypic response to one of sporadic inheritance by means of cytoplasmic particles, such as plasmagenes, and thence to the final phase of attachment of the particle to a gene and incorporation in the Mendelian system of inheritance of the nucleus.

The most critical stage in the adaptive process is probably that leading up to the development of a plasmagene, or comparable particle, capable of multiplication within the cytoplasm. There is now some evidence, in both animals and plants, that this stage can be completed in a comparatively small number of generations. Waddington (3), for example, by subjecting puparia of *Drosophila melanogaster* to a temperature of 40° C., obtained individuals that were phenocopies for the character " crossveinless ". From the 12th generation onwards the character began to appear in flies from puparia that had not themselves been heated. Darlington & Mather (2) cite as evidence for the particulate transmission of plasmagenes, the hybrid of *Epilobium luteum* × *hirsutum*, which is male sterile, when *E. hirsutum* is the pollen parent. After back-crossing with *E. hirsutum* for 14 generations, some male fertile shoots appeared in about

1 in 400 plants. Self-pollination of these plants gave fewer male sterile progeny, when the male fertile flowers were used instead of the male-sterile flowers. If plasmagenes controlling male fertility are ever present in the pollen of *E. hirsutum*, why should they wait for 14 generations before passing over with the male generative nucleus? It would appear that the evidence has been misinterpreted and that what took place was the reorganization of certain metabolic processes controlling male fertility, by the genes of *E. hirsutum*, in the presence of the cytoplasm of *E. luteum*. In other words, an adaptation took place in the adverse microenvironment of the *E. luteum* cytoplasm.

What was the nature of that adaptation?

In recent years, a number of investigations have been made of the effect of boron on pollen fertility and this element has been shown to be necessary for pollen germination in various fruit trees (4), in *Corylus* (5) and in *Forsythia* (6). The connection with the boron content of the soil has been demonstrated by Antles (5). Moewus has worked out, in some detail, the biochemistry of fertility and heterostyly in *Forsythia*, where boron is linked with the enzymes that split quercitin and rutin, respectively. One may hazard a guess, that the regaining of fertility in the *Epilobium* hybrid was due to the development of an enzyme system in which boron may have been concerned.

It is now well established that many mineral elements are essential to the metabolism of animals and plants. According to a recent estimate 72 elements are utilized. In its active condition in the cell, an element is often in a non-ionic condition, linked or chelated to complex molecules, like magnesium in chlorophyll, or cobalt in cyano-cobalamin—vitamin B_{12}. Fixation of an element in the non-ionic condition enables the plant to accumulate it against a concentration gradient. A concentration many hundreds of times greater than that in the surrounding environment may be attained, as with iodine and gold in certain seaweeds, lithium in tobacco and barium in Brazil nuts. In such manner, adequate quantities of essential elements are accumulated. Absence or deficiency, as well as excess of an element, may have a profound effect on the metabolism of a plant or animal. Many of these effects are not manifested by a change of form, although they may be. The whiptail symptom of molybdenum deficiency in *Brassica* crops is a case in point, where a failure of the lamina of the leaf to expand is the result (7). That the mineral content and balance of the elements in the soil does produce morphogenetic effects in the course of time is evidenced by numerous field observations, although the physiology of their origin has not been worked out. We find, for example particular species or varieties associated with mineral veins containing metals such as zinc, lead or copper. I, myself, found a new species of *Westringia* (*Labiatae*) apparently confined to a single stratum of the nearly vertically tilted rocks of the Ordovician series in the auriferous area near Bendigo, in Victoria. In Australia, also, it is a well-known phenomenon, that the line of junction between two geological formations is often clearly marked by a floristic change, one species of Eucalypt abruptly replacing another. There is abundant empirical evidence, then, that the mineral content of the substrate may set up effective adaptation pressures.

The water relationships of the environment give rise to another set of adaptation pressures. There are interactions between the availability of water, the superficial geology and the uptake of minerals by the plant. The final result may be the production of a cline, affecting one or more characters, of which that of leaf breadth in *Acacia acuminata* in Western Australia is an example. I will refrain from discussing this aspect further, at present and pass on to the effects of temperature, which raise some points of fundamental importance.

The "role of plasmagenes in acquired adaptations" was recently discussed

by Crosby (8). He considered a hypothetical case of a plant adapted to relatively mild conditions, but provided with a plasmagene that assisted it in adapting to low temperatures. The plasmagene could have arisen as a response to an adaptation pressure resulting from a deterioration of climate, so the origin of the plasmagene may be conceded, although it was not discussed. Crosby considered it necessary to make a "fundamental assumption", namely, that with the lowered temperature, the rate of reproduction of the plasmagene did not fall to the same extent as that of the cells. This would lead to an accumulation of the plasmagene and hence an increase in resistance to cold. The cell is a physico-chemical system and must necessarily obey physico-chemical laws. A consideration of the Le Chatelier principle would make it clear that Crosby's fundamental assumption is superfluous. The Principle may be stated as follows :

> When any influence, or factor, capable of changing the equilibrium of a system is altered, the system tends to change in such a way as to oppose and annul the alteration of this factor.

Temperature, light, water relationships and the mineral content of the soil, all will be governed by this principle. It must determine the adaptive path taken by an organism when its environment changes.

The effects of temperature are more precisely defined by Van't Hoff's Principle of Mobile Equilibrium, which can be regarded as a special case of the Le Chatelier principle. Van't Hoff's principle may be stated as follows :—

> Any change of the temperature of a system in equilibrium is followed by a reverse thermal change within the system.

There are three possible alternatives, depending whether the reaction is exothermic, endothermic, or indifferent to thermal changes. A lowering of the temperature would favour an exothermic reaction, which would fit the case postulated by Crosby. The rate of reproduction of the plasmagene would increase and it would tend to accumulate. The plant would continue to adapt with falling temperatures. In fact, an orthogenetic development would be initiated.

It will be evident from the argument presented above, that the operation of the Le Chatelier principle will tend to cause orthogenetic evolution, not only when temperature is the main factor, but also where other environmental conditions are involved. The translation of these physicochemical principles into morphological terms may not at once be obvious. however. I have time to consider but one example.

A few years ago I described the British elm, *Ulmus coritana* (9) which varies in leaf shape, with broad round-leaved individuals in the south of its range and a gradation to relatively long narrow and very asymmetrical leaved individuals in the north. There is, in fact, a south-north topocline. I was unable to point to any one environmental factor to account for this cline, but there must be a temperature gradient over the range of the species. Let us consider what might happen if temperature were the operative factor. A metrical examination of the leaf shapes indicated, that leaves behave as if their growth was controlled by two factors, one governing breadth and the other length. Suppose the biochemical processes leading to the synthesis of the growth hormone governing breadth were predominantly exothermic and those for length endothermic. Then a temperature change would cause a differential change in leaf shape, which would be enhanced the greater the difference in temperature. The observed facts would fit this theory, but it remains pure hypothesis, though. presumably open to experimental study.

To sum up, recent researches have demonstrated, in unicellular organisms, environmental responses that become heritable after a lag period. Similar responses take place in the cells of multicellular organisms, but they cannot be

inherited until their biochemical mechanism becomes linked to a transmissible particle, such as a plasmagene. The plasmagene ultimately becomes attached to a gene and incorporated in the nucleus. The integrated genetic system of the nucleus is the end product of this evolution, controlling the development, metabolism and inheritance of the organism. Never the less the major evolutionary process is the acquirement and fixation of adaptive modifications in response to environmental changes. The operation of physical laws tends to make this evolution orthogenetic.

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Inheritance of Acquired Characters.

By C. H. Waddington, Institute of Animal Genetics, Edinburgh.

(With 5 Text-figures.)

Ever since the beginning of scientific thought it has been recognized that one of the major problems for biology—indeed for our most general ideas about the universe we live in—is that posed by the appearance, in the living realm, of phenomena which have tempted many people to suggest that they are the expression of some form of Will or Design operating during organic evolution. With the rise of genetics and the discovery of the apparently undirected process of gene mutation, it has become apparent that these phenomena can be given at least a formal explanation as the results of Darwinian natural selection acting on the products of random mutation. If the types of mutational event which can occur are uncontrolled and unrestricted, then we can suppose that, in a long enough period of time, any type of gene at all will occur in an animal lineage. Such a process is theoretically omnipotent, in the sense that it could bring about any modification whatsoever in the structure and functions of an animal. It therefore suffices to provide a formal explanation for all those cases in which the delicate co-ordination of the various parts of an organism with one another, and the subtle way in which the organism's structure fits in with the demands of its mode of life, have been held by some to suggest an element of design in natural processes. As has been frequently pointed out, random mutation and natural selection together constitute a mechanism for generating states of high *a priori* improbability.

Nevertheless, one may feel not wholly satisfied that this conventional

theory contains the whole truth. It gives some sort of an explanation of anything that may occur in evolution. But perhaps one may think that it does not give very much explanation of anything. Granted that natural selection and random mutation, by labouring mightily, might generate any given state of high improbability, may there not perhaps be other contributory factors which can somewhat lighten their task? Many people have felt that strong indications of the reality of some other element in the situation are to be found in the frequent occurrence of a genetically controlled adaptation of a species to local conditions. It is quite often observed that if members of a species are transferred from the environment A, in which they normally live, into another environment B, they develop during their lifetime some modifications similar to those found in members of the species which normally live in B. If these transferred individuals, or their progeny, are removed back again into environment A, the modifications induced by B commonly disappear. On the other hand, when individuals from the population native to environment B are moved into environment A, they frequently do not wholly lose the features characteristic of the B type. These B characteristics are then, to some extent, hereditarily fixed in the B population, which has evolved what Turesson has called an ecogenotype, adapted to the particular demands of the B environment. Now one can ask, is it really plausible to suggest that the fact that individuals living in A will, if transferred to environment B, develop characteristics similar to the B-adapted population, is wholly irrelevant to the process of evolution? For this is what would follow from the theory of random mutation and natural selection if it is taken at its face value, and without any further elaboration.

Many people have felt that this step in the argument is not a plausible one. They have usually proceeded to argue that an environmental stress, such as that exerted by the B conditions on the A population in the example above, must be supposed eventually to produce, if continued for long enough, not only developmental modifications, but actual hereditary alterations which act in a similar manner. It is comparatively easy to invent theoretical schemes by which this might occur. In recent years we are coming more and more to conceive of the genes, on which heredity depends, as particles engaged in active metabolism, a metabolism which is involved both in their operations in directing developmental processes, and in the synthesis of new genes which are required as cell division proceeds. Phenomena such as the formation, for instance in bacterial cells, of induced enzymes adapted to the particular substrates present, provide models which easily tempt anyone with imagination to work out theoretical schemes by which environmental demands might evoke related modifications in the genes. However, all such mechanisms remain entirely speculative at the present time. In fact, they are not merely speculative but, so far, quite unnecessary. There is no compelling experimental evidence which forces us to believe that environmental stresses ever do alter genes in such a manner that they function in some way relevant to the environmental demands: and it is, of course, well known that there have been several attempts to find such processes which have failed to discover them.

There is, however, another line of thought along which one can proceed, starting from the basis that the direct developmental modification of an organism can hardly be supposed to be absolutely irrelevant to the process of evolution. One would, on general grounds, expect the capacity of an organism to respond to an environmental stress to be under genetic control, and it is reasonable to suppose that in any large population there will be some variation between individuals in this respect. If a particular response to some stress is adaptive, that is, produced some selective advantage in the stress conditions being responded to, then natural selection will favour those individuals in which capacity for this type of response is highest.

One can fairly easily set up an experiment which provides some sort of a test of this suggestion. I have not, so far, devised suitable conditions for producing a response which is really adaptive in an organism which is easy to breed through many generations. However, one can apply artificial selection in favour of environmentally produced responses which would not be of adaptive value under natural circumstances. For instance, if Drosophila pupae are subjected to a hot shock some individuals respond by developing morphological abnormalities in the wing venation. These are almost certainly of no adaptive value, but one can artificially select for them. Fig. 1 shows the results of the first experiment of this kind which we carried out. Selection was practised for, or against, the capacity of Drosophila to respond to a particular hot shock by the absence of the posterior cross-vein. The results in the first four generations are omitted from the figures, since at that time we used a hot shock of a different

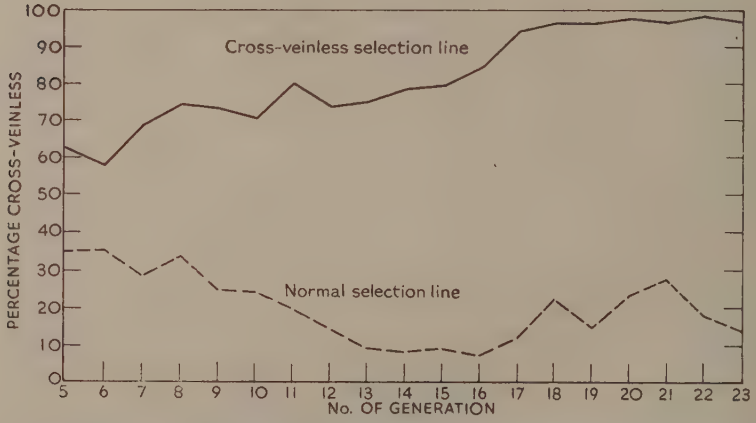

FIG. 1.—Selection for and against the tendency of *Drosophila* to develop with a broken posterior cross-vein after a high-temperature shock to the pupa. (From Waddington, O. H., 1953, *Evolution*, **7**, 118.)

length to that employed for the rest of the experiment. It will be seen from the top line in the figure that the percentage of animals showing the response gradually increased. Now a very important point that emerged was that from generation 12 onwards we began to find a few cross-veinless flies among the brothers and sisters of the individuals which had been subject to the hot shock. That is to say, the environmentally produced abnormality was beginning to appear in untreated individuals which had never lived in anything but the normal conditions. From generation 12 onwards the frequency of these individuals increased. If they were taken and bred together, without any further application of a hot shock, we could rapidly build up strains in which nearly all the individuals lacked the posterior cross-vein. In these strains the phenotype, which originally would deserve the name of an acquired character since it was only formed under the influence of a particular abnormal environmental stress, was now genetically fixed and appeared without any need for an external precipitating stimulus. Such a process has been called "genetic assimilation".

Similar experiments have since been conducted by Mrs. Bateman in our laboratory. She has used a number of different initial stocks and selected for several different types of developmental abnormality. In all the cases studied she was able to achieve the genetic assimilation of the originally acquired character. In Fig. 2 the upper line shows the progress of selection, again for the absence of the posterior cross-vein, starting from a mass bred Oregon-R stock. It will be seen that even when the duration of the temperature shock was reduced from 4 hours to 3 hours, and finally to two hours, the frequency with which the developmental abnormality occurred increased to over 90 per cent. An important point is brought out by the lower line in Fig. 2. When selection of the same type was practised on an inbred line derived from the Oregon-R strain, there was no increase in the frequency with which the abnormality appeared. This is good evidence that in this case at least the genetic

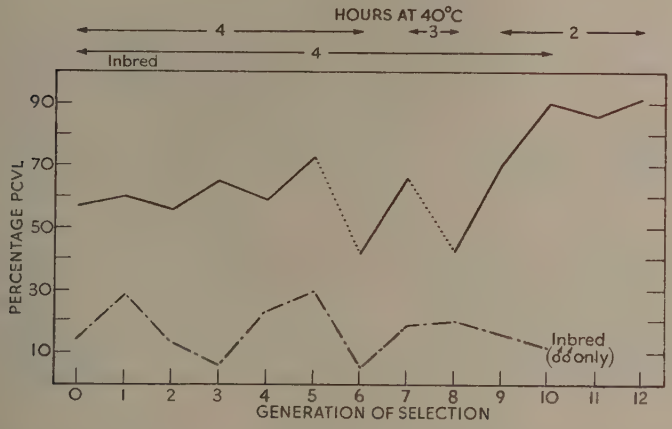

FIG. 2.—Selection for frequency of crossveinless types, following a heat shock, in mass-bred Oregon stock and in an inbred stock. (From Waddington, *The Strategy of the Genes*, 1957.)

factors responsible for the increase in susceptibility and for the eventual genetic assimilation of the character did not arise during the period of the experiment, either as a result of the treatment, or in any other way. One must therefore suppose that these factors were all present in the initial population. What selection for the environmental response has achieved is the sorting out of these factors, and the bringing of them together into genotypes which eventually contain many of them. If this is true, and the genetic factors responsible for the assimilated character were all present in the initial population, then, if we examine enough of that population, we should find some individuals in which, by chance, sufficient of the factors have come together to produce the abnormal phenotype in the normal environment. In the stock with which the first cross-veinless experiment was done we never actually found any cross-veinless individuals in the starting population, but this may well have been because we did not examine enough of them. In some of the other populations studied, a low percentage of the abnormal type has been found right from the beginning. For instance in Fig. 3, which shows the results of selection for the absence of

posterior cross-vein in a wild Edinburgh stock, there were a very few cross-veinless individuals, less than 1 per cent, in the initial population ; and their frequency increased slowly as the selection for the response to the environmental stress progressed.

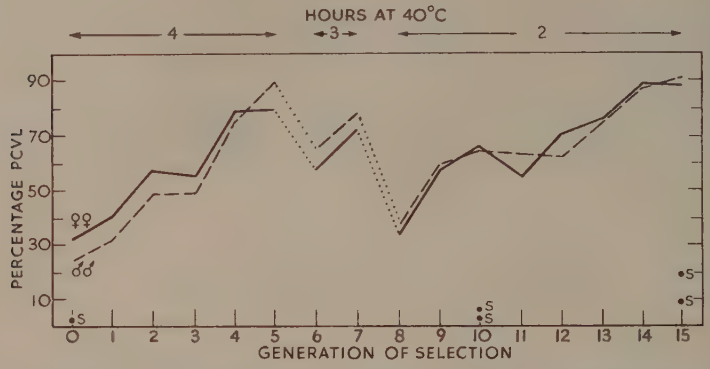

Fig. 3.—Selection for crossveinless, in an Edinburgh stock. The frequency of spontaneous crossveinless is shown by the points labelled S. (From Waddington, *The Strategy of the Genes*, 1957.)

These facts find a simple explanation if we suppose that genetic factors, which facilitate some particular developmental response to an environmental stress, also act in the direction of that type of modification even in the absence of the stress. The environmental stress acts to reveal, and to expose to natural selection, genes which were already present in the population, but whose action is normally only sub-threshold in intensity and therefore imperceptible.

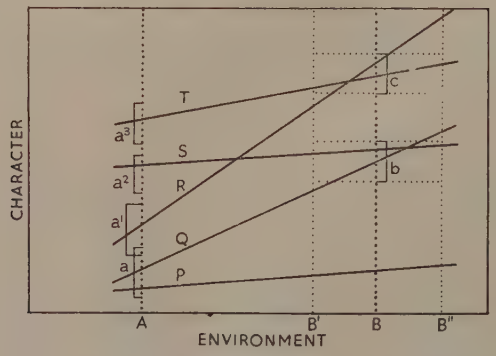

Fig. 4.—The two phases of genetic assimilation. (From Waddington, *The Strategy of the Genes*, 1957.)

We can probably regard the whole process of genetic assimilation as taking place in two phases. These can be illustrated in Fig. 4. Suppose that we start with the population living in environment A and exhibiting a range of phenotypes " a ". Let the environment now be changed to B. Let us suppose that

an increase in the character indicated on the diagram is of adaptive value. Some of the genotypes in the population show little response to the environmental stress, line P. Others will be more sensitive, line Q. The latter will be selected. By the shuffling and recombination of genes from individuals which respond something like Q, we may build up genotypes whose response is something like R. These, if returned to the initial environment A, will give a population whose phenotype falls in the range " Al "—these are partly outside the range of original population and we could say that some degree of genetic assimilation has occurred. The process which has been at work is one of " normalizing selection " towards the phenotype which is of highest selective value in environment B. A second process could, however, supervene if it was of selective advantage to the organism to show little variation in response to minor fluctuations of the environmental conditions around those of B. There would then be selection for genotypes whose responses are of the kinds indicated in the

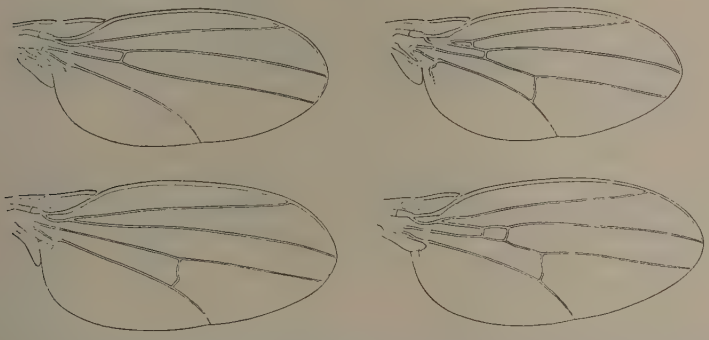

FIG. 5.—Four types of crossvein abnormality; absences on the left and additions on the right. (From Waddington, *The Strategy of the Genes*, 1957.)

lines S and T, which are relatively insensitive, to environmental variation between B′ and B″. On return to environment A such genotypes would show a much higher degree of genetic assimilation. The process at work here can be referred to as " canalizing selection ", tending to stabilize an optimum value in conditions near to those of environment B. This type of selection is, in effect, what we have produced artificially when we select, in the later generations of an assimilation experiment, those individuals which show the abnormal phenotype without the environmental stress.

There is a further process, over and above the normalizing and canalizing selections, which may also occur. Fig. 5 shows four varieties of abnormality in the cross-veins of Drosophila. In most normal wild-type stocks submitted to a temperature shock in the pupal period, all four types of abnormality occur. If selection is practised for any one particular abnormality, its frequency increases, while the frequency of the others does not increase at the same time and may even be reduced. One can therefore obtain genotypes into which any particular one of these abnormalities has been assimilated. It seems probable that one can generalize from this experiment and deduce that, if in a population the original response to an environmental stress is of only slight adaptive value, there is likely to be genetic variation available which will make it possible for selection gradually to modify the response so that it becomes of greater advantage to the organism.

This point raises one of the most puzzling questions which remains in one's mind in connection with the whole problem of the inheritance of acquired characters. How does it come about that the responses of an organism to environmental stress are so often of adaptive value? It is, of course, by no means the case that they always are useful in this way. For instance, the vein abnormalities we have worked with almost certainly are of no adaptive value. On the other hand, we find surprisingly frequent examples of two probably closely related phenomena. In the first place, a simple stress may call forth a simple response of adaptive value; for instance a lowering of the oxygen tension may elicit a higher concentration of blood corpuscles. Secondly, a complicated stress—such as that, for instance, of digging with the fore-legs—calls forth a complex, but co-ordinated, series of responses in the structure of the skin of the hands, in the claws, and in the skeletal and muscular elements of the fore-limbs and shoulder girdle. We still have a very imperfect understanding of the mechanisms by which these effects are produced, or of the manner in which evolution has brought them into being. In very general terms we may say that embryonic development always involves epigenetic interactions between parts—so that, for instance, changes in skeleton are nearly always accompanied by changes in musculature and vice versa. Following on this we may suppose that evolutionary forces, acting over a long very period of time, favour those types of epigenetic interaction which result in sets of correlated changes which tend to be of adaptive value. For instance, those in which a shortening and thickening of a given limb bone tends to modify the associated muscles in a way appropriate for the new functional demands that will be made on them. Such general arguments, however, require much further elaboration and some experimental testing before they become very convincing.

In summarizing, I should like to repeat the statement which is printed on the programme.

Summarizing, the first point to emphasize is that the capacity of an animal to respond to a given environmental stress by a particular type of developmental modification is a function of its genotype. If the capacity is favoured by selection, a higher proportion of the population will respond in this manner in later generations. It has been shown in several cases in Drosophila that selection for the capacity to respond to stress in a certain way is accompanied by the appearance, and increase in frequency, of individuals which exhibit the favoured phenotype even in the absence of the environmental stress. By continued selection for the developmental response (or, more quickly by the selection of the individuals which show the phenotype in the absence of the stress) stocks may be built up in which the character, which was originally an "acquired" one, is developed even in a normal environment. This process has been called "the genetic assimilation of an acquired character". It has been interpreted as indicating that the genes which facilitiate a given developmental response to stress also have a tendency to modify development in a similar manner in the absence of the stress, this tendency being only of trivial or sub-threshold intensity until genotypes have been built up in which a considerable number of similarly acting genes have been collected together. Further, it can be shown that selection can also modify to some extent the precise character of the response to stress; this makes it possible for a response, which was originally only imperfectly adaptive, to be gradually "tuned" more closely to the requirements of the animal's life.

These experiments reveal a mechanism, operating in a perfectly "orthodox" Mendelian way, by which characters which at an early stage of evolution are produced as responses to environmental stresses may at a later stage no longer require any external precipitating stimulus. The most important question which remains for discussion is how it comes about that so many of

the responses of animals to environmental stresses are adaptive, i.e. have positive selection value in that environment. Probably the answer will be found to be based on two considerations : (i) development must (for the sake of economy) be epigenetic, and involve interactions between parts ; (ii) selection, acting on a macro-evolutionary time scale, will tend to favour those types of epigenetic interaction which offer the possibility of adaptive response to stresses (for example, it will favour systems in which increased use of a component is followed by the appearance of more of it rather than by its wasting away).

General Discussion

Dr. **W. B. Turrill** said that in his genetical and cultural experiments with a limited number of species of flowering plants he had no evidence of the transmission to subsequent generations by sexual reproduction of characters modified in an individual by environmental conditions.

He would much appreciate the comments of cytologists acquainted with bacteria on the statment he understood Prof. Cannon to make that bacteria had no nuclei, no chromosomes, and no sexuality but at most only " simulacra " of these. Was not the tendency to bring bacteria into line with higher organisms in these respects and had not hybridisation been recorded even for viruses ?

Dr. **M. L. R. Pettersson** welcomed the occasion on which the Society dedicated to Linnaeus was now turning its attention to the behaviour of organisms much smaller than those able to be considered two centuries earlier ; since, with the short generation times and small size of micro-organisms and of *Drosophila*, many biological problems may prove capable of solution more quickly and more economically.

In contrast to the attitude of Prof. Graham Cannon, he noted that recent work suggests that both bacteria and viruses, as well as larger cells, possess genes, and genes maintained in a constant linear order. As a rough generalization, perhaps each virus contains several tens of genes, each bacterium several hundreds, while each ordinary cell several thousands of genes. Essential reading for biologists not specializing in this field are the short and lucid books by Catcheside (*The Genetics of Micro-organisms*, 1951) and by Haldane (*The Biochemistry of Genetics*, 1954).

Mr. **P. F. Mattingly** said that a very beautiful experimental demonstration of the existence of a linear arrangement of hereditary factors in *Escherichia coli* had been put forward by certain French workers. This work had been described by Professor Catcheside in a paper read by him at a joint meeting of sections D and K at the recent British Association meeting at Sheffield.

Dr. **S. M. Manton** said we have heard a lot about isolated characters of organisms which exhibit variation and which are capable of experimental study. Valuable as these studies are it must be remembered that an animal in nature can seldom be concerned with changes in single isolated characters, whether these be morphological, physiological or appertaining to behaviour. So very many characters are intimately correlated in the harmonious working of the whole that a change in a single character alone, if such occurred, might be ineffective. An example may make the point clear. Slow moving centipedes have tergites of successive segments of similar lengths, but fast moving centipedes have evolved tergites of alternate lengths, the heteronomy being developed to different degrees in several independent groups. The functional significance of this striking feature is now known, it enables body undulations at fast speeds to be minimized. Now it could be suggested that the character

tergite length might be controlled by a complex of genes, and that natural selection might operate on chance mutations in tergite length. However, the mechanical usefulness of tergite heteronomy arising in this way *would be nil*, unless a great many harmonious changes occurred *simultaneously*. The morphology of some 300 muscles of centipedes has been examined, and changes in extrinsic leg muscles, in dorsal longitudinal muscles, in pleural muscles, in deep dorso-ventral and oblique muscles, and changes in joint morphology of both legs and trunk are *all* bound up with tergite heteronomy, and enable this striking morphological character to operate in the way in which it does. Presumably each of the many features grouped under above headings may be controlled by a gene complex. It follows that the complexity of the genetical changes, which presumably might arise (*a*) by chance and (*b*) simultaneously to give a basis for natural selection leading to the evolution of tergite heteronomy, must be prodigious, indeed so prodigious as to suggest that the concept may need reconsideration.

Mr. **J. S. Kennedy** said that it seems to be the general assumption that, while good evidence is now available for the inheritance of acquired characters in micro-organisms, one can still only speculate about the possibility in Metazoa. But in entomology, especially applied entomology, this question so far from hypothetical, is an important practical one. The idea that the germ-plasm is entirely independent of the soma has had to be jettisoned in a number of insect cases (e.g. locust phases and other instances of polymorphism, and diapause in various insects) ; but the very fact that the pre-requisite for doing so has often been the special incentive for open-mindedness which comes from economic interest in a problem, shows that we have here a dogma which is an impediment to the advancement of knowledge and ought to be dropped.

Dr. **A. C. R. Dean** in replying to a question on the bacterial nucleus said that this was still a controversial issue. Dr. Dean further said that bacterial strains had been cultivated for a very long time in a simple defined medium and that the behaviour in this medium before and after the addition of drugs or change in the carbon source was compared. Mutation-selection theories as well as the hypothesis of automatic adjustment in response to the environment, since many microbiologists have prefererred the former explanation for bacterial adaptations of a similar nature were always considered.

INHIBITION OF GERMINATION OF THE WHITE MUSTARD BY BRYONY JUICE [Exhibit.]

By I. Henry Burkill.

The inhibition of germination of seed of the White Mustard (*Brassica alba* Boiss.) by contact with juice from the berries of the Common Black Bryony (*Tamus communis* L.) was exhibited. Two experiments were described ; in one the juice was squeezed from ripe berries on to mustard seed that had been given enough water for germination ; in the other on to mustard seed that had been germinated two days earlier. In the first, germination was completely inhibited ; in the other, growth was stopped. From the second experiment, the poison was washed away after two days ; it was then observed that a very slow and inadequate growth was resumed.

The juice from berries of the Black Nightshade (*Solanum nigrum* L.) was found also to inhibit germination.

The speaker suggested that the active substance might be the saponin which is present, adding that the next step should be to extract the saponin and try

its effect. If a chemist could be persuaded to do this, he should at the same time prove the presence or absence of sugars. Bryony berries are not distributed by birds : there is nothing except the colour to attract them and the poison is a repellent. The experiments were part of an enquiry into the function of the juice (if there be any, or if it be merely what is left from the business of ripening the seeds).

DISCUSSION

Dr. **C. R. Metcalfe,** commenting on Mr. Burkill's exhibit, drew attention to the fact that the presence of germination inhibitors in fruits and seeds had been discussed by Professor Audus in his book entitled *Plant Growth Substances*. The subject had also been reviewed by Evenari (*Bot. Review*, **15** : 153–194 ; 1949). It had also been confirmed by Miss E. M. Slatter's work at the Jodrell Laboratory at Kew (*Kew Bull.*, 425–430 : 1950) that the embryos of certain bearded iris hybrids can be made to germinate when they are removed from the inhibiting influence of chemical substances in the endosperm and grown in sterilized cultures on nutrient agar. It was clear from the literature that the occurrence of germination inhibitors in fruits and seeds is very widespread, and that the chemical nature of the substances responsible is very varied. Mr. Burkill's exhibit was of interest because it drew attention to a phenomenon that was worthy of further investigation, and also because the presence of a germination inhibitor did not appear to have been previously recorded in the fruits of *Tamus communis*.

THE FISHERIES LABORATORY, LOWESTOFT

AN EFFECT OF LOW TEMPERATURE ON THE OSMO-REGULATORY ABILITY OF THE COD (*GADUS CALLARIAS*) IN ARCTIC WATERS. By P. M. J. Woodhead & A. D. Woodhead.

Part I (*Communicated by P. M. J. Woodhead*).

Since the war the Fisheries Laboratory, Lowestoft, has been carrying out research on cod (*Gadus callarias*) in the Arctic. This work has mainly been done in the Barents Sea, particularly in the region of the Bear Island-Spitsbergen Bank. During the summer months the fish are caught over wide areas of the Bank in shallow water, feeding very heavily on the rich swarms of zooplankton and on the capelin (*Mallotus villosus*). In the autumn cold Arctic waters flow south and west across the Bank covering it for the winter and spring. The cod then leave the Bank for deeper waters and appear to avoid the cold water masses. This pattern of extension over the shallow areas of the Bank to feed in the summer, followed by a southward contraction of the population in autumn to the deep water overwintering areas, is repeated annually until the fish become mature, when nine to ten years old. Maturing fish then pass through the deep overwintering areas of the immatures and south to the north Norwegian coast to form the vast spawning shoals on the Lofoten grounds.

We are interested in the finer details of the distribution of the fish, particularly with reference to environmental changes. Details of distribution have been obtained by trawling surveys, and, more recently, by using echo-sounders to survey the population. The environmental factor which has been most studied is temperature, an obvious choice since the Arctic waters form cold fronts in this region with the warmer waters of Atlantic origin. Paying

catches of cod (i.e. more than 1½ tons per hour) are not taken in water below 2° C., except in the summer months of July–September when the fish may enter colder water, down to about 0° C. In May–June immediately prior to the feeding season, and again in October–December, the distribution of the cod is particularly interesting. At these times the fish are caught at rates of up to 15 tons per hour at the edges of the Bank, and are localized along the boundary between warm and cold water masses, the concentration of the fish often increasing as the temperature gradient becomes steeper.

Although the relation between temperature and the distribution of the cod has been stressed, this relationship need not be brought about directly by temperature, for if the fish remained passively within the warm Atlantic water mass, then they would appear never to go below a certain temperature. It was therefore of considerable importance to our complete understanding of the movements of the fish to know whether to consider this as a real effect of temperature.

Part II (*Communicated by A. D. Woodhead*).

The effect of temperature on the distribution of the fish often appeared to be a direct one and a hypothesis was sought to explain the facts. It was thought probable that the fish reached a physiological limit at 2° C. The sparse data available suggested that at low temperatures the osmo-regulatory mechanism, maintaining the fish's blood-salt content at about one-third of that of the seawater, broke down, resulting in death after some time. If temperatures below 2° C. have this effect on the cod, analysis of blood taken from the few fish which are caught in cold water would show a salt content increased above normal values. However, such a hypothesis would have to take account of the occurrence of large numbers of cod at temperatures down to 0° C. in the summer months. A number of workers have shown that the osmo-regulatory ability of fish can vary with the state of activity of the endocrine glands, and it might be expected that if low temperature acts through the breakdown of this mechanism, then the lower lethal temperature would also vary with activity of the endocrine glands.

Analyses of blood from cod caught at temperatures above and below 2° C. bore out the hypothesis. Analyses for sodium, potassium, and chloride, and total salt content (as estimated by freezing-point depression) were all higher, on the average, in the fish caught in cold water, often as much as 30 per cent higher than the normal values. However, this did not apply in the summer months when there were no significant differences in the results of the analyses. Therefore it does seem that cod taken in waters below 2° C. in winter and spring are in a state of osmotic imbalance, whereas during the summer fish are able to enter these colder waters and still maintain themselves in normal salt-balance.

Various endocrine glands were taken from the fish and have been examined histologically. So far only the thyroid has been fully investigated. Thyroid activity has been shown to depress the osmo-regulatory ability of some fish ; in cod it becomes active just as they are about to leave the cold water. However, it re-enters the resting condition in March-April, some two months before the fish are able to enter the colder water. A complication is that the fish are in very poor condition in early spring, having fed, but lightly, if at all, for about five months. Starvation is known to raise the lower lethal temperature in fish and it may be that even though the thyroid is inactive the cod must begin to feed again before they can enter the cold water.

Alternatively, some other gland may be the main controller and investigations now in progress should reveal whether this is so.

Marine Fish Larvae and the Osmotic Hazard

By J. E. Shelbourne.

During current investigations into the laboratory conditions necessary for consistently successful marine fish rearing it has become increasingly evident that the osmotic hazard confronting the early larva is much greater than that facing the adult. Both larva and adult live under an osmotic strain, having internal salt concentrations roughly $\frac{1}{3}$ that of the surrounding seawater.

The integument of the plaice larva is a thin syncytial membrane, partly separated from the muscular axial tissue by a voluminous subdermal space. Its ability to do osmotic work can be critically affected by external changes in the physicochemical environment, and by the internal energy supply. Unfed larvae quickly succumb to the osmotic strain, after complete yolk loss. The thick, secretory, scaly skin of the adult, on the other hand, is virtually water and salt-proof, osmotic leakage being restricted to the gill surface and oral membranes. Temporary starvation is never critical; food reserves provide energy for osmotic needs over long periods.

In both young and old, regulatory mechanisms are necessary to offset water loss and salt gain under the osmotic gradient. The adult swallows seawater to make good water loss. The larger and less mobile ions, e.g. Mg^{++}, Ca^{++}, SO_4^{--} are eliminated with the faeces; water and the remaining electrolytes pass through the gut wall into the blood stream. Excess chloride is secreted to the outside by special cells in the gills. The essential structural requirements for this mechanism of salt control, are not generally present in emergent marine fish larvae. The blood circulation is not yet complete and the gill filaments are absent. Where then, and how, do marine larvae regulate their internal chloride concentration?

Copeland[1] used a modification of the Leschke chloride test, to investigate the chloride secretory cells of the adult *Fundulus heteroclitus*. My histochemical methods stem from this source. Living yolk-sac larvae of plaice, cod and dab were washed in distilled water for 3 secs., then plunged into a dilute acid-silver nitrate solution in a dark room, under a safe light. After 3 hours impregnation, the larvae were washed thoroughly in distilled water to remove all traces of silver nitrate; immersed in dilute photographic developer solution for 1 hour; rinsed; fixed in hypo for $\frac{1}{2}$ hour; washed, dehydrated, cleared and mounted. Light precautions must be very strict until the hypo stage. Silver deposition is greatest in the yolk sac region of the integument and at the fold of the marginal fin. A remarkable and consistent feature of treated larvae, is the fine, heavily stained continuous network ramifying over the whole integument. This reticulum bears globular, corpusculate, nucleated bodies on its meshes, aggregations of which form the characteristically heavy deposits around the yolk sac and in the fin fold. Smaller stained particles lie between the meshes. The network clearly has different properties to the rest of the unstained integument and the lightly stained main axial tissues. If this conspicuous and regular pattern truly represents chloride distribution in the marine fish larva, then the whole thin integument, particularly around the yolk sac, is intimately concerned in salt regulation. The integument of a living larva, in bad conditions under the microscope, is extremely active. The globular bodies become very prominent, and can be frequently seen to discharge their mucoid contents to the outside. Such discharge is always accompanied by local loss of integumental surface area, and is probably responsible for the normal diminution of the outer yolk sac during yolk utilization.

The specificity of silver nitrate, as a histochemical reagent, is in some doubt.

(1) Copeland, D. E. (1948). *J. Morph.*, **82**, 201.

As well as reacting with tissue chlorides to produce silver chloride, unstable in the light, silver nitrate can be reduced directly to silver by vitamin C. Artefacts are often produced by silver salt fixatives, although mild larval fixation in Baker's Ca-formaldehyde just before silver impregnation, serves to emphasize still further, the regularity of the larval network. Copeland's technique assumes the initial formation of insoluble silver chloride in the tissues, made more visible by controlled reduction in developer solution. I have obtained some evidence to support this assumption, by using known solvents of silver chloride.

If silver-fixed larvae are treated with 0·1 N solutions of ammonia, sodium thiosulphate or sodium cyanide after impregnation, negative results are always obtained on subsequent development, due presumably, to dissolution of the precipitated silver chloride. Larva fixed in 5 per cent chloride-free formalin for 2 minutes, followed by normal treatment, give positive results. Formalin fixed larvae allowed to remain in formalin or distilled water for $\frac{1}{2}$ hour, give negative results, suggesting that the cellular reactant is only loosely bound in the integument, and quickly diffuses out after death in chloride-free preservative.

An attempt is being made to test this histochemical evidence using one of of the two available radio-isotopes of chlorine.

SYMPOSIUM ON AEROBIOLOGY*

The Automatic Volumetric Spore Trap and Examples of its Use in Plant Pathology. By Dr. J. M. Hirst.

Accurate information about the spore content of the air is important in plant pathology and allergy. Spore traps in common use give misleading results, for their catches depend greatly on wind speed, the size of the spores and of the traps themselves. Suction traps not only catch more spores but the catch is more representative of the total population and their efficiency less variable. The traps we have used impact spores from an air stream on to a slowly moving sticky microscope slide so that a day's catch can be analyzed at hourly intervals. Results show that the composition of the outdoor air-spora is continuously changing with the weather and the behaviour of different organisms. Basidiospores form an unexpectedly large part of the population. Particular attention has been paid to the measurement of spore liberation from the fungi causing potato blight and apple scab. This information helps to define the conditions required for infection, and so to improve the timing of control measures.

The Incidence of Atmospheric Pollen and Spores in Great Britain, Considered from the Point of View of Allergy. By Mr. H. A. Hyde.

The study of atmospheric pollen and spores in relation to allergic disease has been pursued at Cardiff from 1942 onwards. The survey methods used have included the "gravity" slide, the Hirst automatic volumetric spore trap, and the petri plate. Data on either pollen or mould spores covering a year or more have been obtained from 19 stations in all.

The phrenology and range of annual incidence of the principal types of pollen and of culturable moulds have been established and the essential validity of the fundamental postulates of pollen and mould allergy has been confimed.

More recent advances include volumetric counts for the principal pollen and some spore types (including studies in diurnal variation as related to clinical observations) and correlations between slide and Hirst trap catches.

* See *Nature, Lond.* (1957), **179**, 890, for further account.

APHID DISPERSAL AND DIURNAL PERIODICITY. By L. R. TAYLOR, Department of Entomology, Rothamsted Experimental Station, Harpenden, Herts.

(With 2 text-figures.)

Visual observation of the aerial movements of such small insects as aphids is of doubtful value by itself for, even over short distances, it is difficult to pick out a flying aphid in winds above about 3 to 4 m.p.h. (about 5 f.p.s.) and considerable errors of judgment are possible especially in estimating the numbers in flight. It is therefore usually necessary to observe such movements quantitatively at second hand by catching the aphids in traps. The difficulty is emphasized when the distances involved are miles rather than feet for it is not then possible to follow lateral movements except those of marked insects released from a point source or those of large insects in swarms such as locusts.

Locust swarms, especially those extending to considerable heights, tend to be displaced down-wind in spite of local movement in other directions within the swarm (Rainey, 1951). If this happens with such powerful insects as locusts, it is also likely to happen with the vast majority of smaller, weaker insects with much lower flight speeds. The flight speed of locusts (*Schistocerca gregaria* Forskål) is of the order of 11 m.p.h. (Waloff & Rainey, 1951), that of aphids less than 1·2–1·5 m.p.h. (Haine, 1955). In any higher wind-speed than this they must move in general with the wind, whatever their orientation to the ground may be, and since wind-speeds above 1·5 m.p.h. predominate, wind-directed flight in aphids must also predominate unless special mechanisms are produced to avoid it.

Insects are present up to considerable heights in the air on many occasions and their number in a unit volume of air, the aerial density, fluctuates from hour to hour. These fluctuations reflect the movement of groups of insects in height, distance and simultaneously in time. Although in the dispersal of the group it is obviously the horizontal component which is most important, it is not convenient to measure this directly with traps for technical reasons such as the difficulties of marking sufficient numbers of insects and of maintaining a series of traps in line downwind. But if we consider a mass of air, say a column extending through those heights at which wind force and direction are fairly constant, it is not difficult to estimate its lateral movement in terms of the wind of which it is a part. If we could now measure the movement of insects into and out of this column—its rate of exchange of insects—it may be possible to estimate the mean time spent by insects in the air mass and consequently their mean lateral displacement.

It is not realistic to consider even small insects entirely as inert particles, but their own flight movements once they are airborne will usually be small compared with the movement of the air mass in which they are contained. Therefore, the lateral rate of exchange of insects between one air mass and another due to this will probably be negligible. The net lateral exchange due to processes such as turbulent diffusion will approach zero if the insects are widespread and movements between adjacent air masses are random. Thus the vertical rate of exchange, within the air mass and between it and the ground, may be treated as the only significant component of the overall rate of exchange.

The vertical rate of exchange of insects in a mass of air changes continuously as the air moves along with the wind. This rate of exchange is reflected in the profile of density on height at a given time ; the changes in the rate are seen in the fluctuations in the density profile with time. These two variables, the fluctuations of density with height and with time, can be measured by trap catches

and it is through them that an approach to the mechanism of the aerial part of the dispersal of aphids may be made in general terms such as may be applicable to other insects. The factors leading to the presence or absence of insects available for dispersal are largely population and behaviour functions more specific to the kind of insect concerned and probably not susceptible to such generalization.

It has not been possible to follow the history of the same vertical column of air as it moves along for the trapping system is stationary and hence subsequent samples are from different air masses ; we therefore assume that the commoner insects caught, those which mainly constitute the catch, are widely distributed. The initial distribution, depending largely upon that of host plants or breeding sites, may be patchy. But turbulent mixing of the air and local flight of the insects will tend towards a more random scatter during the time taken to collect a sample.

Aerial insect density has been measured at each hour throughout the day and night using standardized traps at heights up to 1000 ft. for many days at Cardington in Bedfordshire (C. G. Johnson & Taylor, 1955). The site is the wide, flat Vale of the Ouse and its physical characteristics have been described in detail by Giblett and others (1932) and C. G. Johnson (1957*a*).

The primary data from the traps at Cardington consist of aerial densities at 24 intervals in the day for each of 5 heights, along with appropriate meteorological records. It is convenient first to deal with the relationship of density to height at a given time. This gives a hollow curve of diminishing density with increasing height to which an empirical equation can be fitted in many instances (C. G. Johnson, 1957*a*).

The expression is :

$$f.(z) = C(z + z_e)^{-\lambda} \quad . \quad . \quad . \quad . \quad (1)$$

where $f.(z)$ is the density at height z ; λ is an index of the gradient of density on height ; and C and z_e are, respectively, a scale factor related to population size and a measure of the departure of the curve from linearity on a double logarithmic scale. It is in the index λ that the equation finds its main direct application especially in relating height of flight to climatic conditions, for it gives a concise indication of the way in which density diminishes with increasing height, the net vertical rate of exchange mentioned earlier. An approximation to this parameter has been shown to be correlated with lapse rate, the rate of change of temperature with height, which is a measure of the stability of the atmosphere and consequently one of the factors concerned in the upward transport of insects (C. G. Johnson, 1957*b*). λ is controlled largely by such physical factors as meteorological conditions and the aerodynamic character of the insect, but flight behaviour must also be involved to some extent since the insects' falling speed depends upon whether or not it is flying. These factors act upon the available supply of insects to produce a given height distribution of the total population.

It is also necessary to assess the total insect content of the column of air. This is done by integration, between standard heights of, for example, 1 to 10,000 ft., either from equation (1) or graphically. The mean height of flight, above and below which there are equal numbers of insects, can be used in a similar way to λ and also is obtained by integration. Finally, by a similar extrapolation, the density at about the level of vegetation may be obtained. Unlike λ, the total numbers and vegetation level density are mainly of value in considering the biological problems involved in dispersal.

Thus the original data can be transformed into the 4 values, mean height of flight, λ, density at vegetation level, and total insect content of the air,

and each of these may be plotted separately against time. It is in the diurnal fluctuations of these statistics that the dispersal processes can be seen and their explanations sought.

The flying population at vegetation level is a balance between the supply of insects by take-off from their host plants, the loss to the upper air-levels, and the loss by alighting. The biological component of this is obviously a large one, for the specific behaviour pattern of the insect will determine its willingness to fly or alight at any particular instant, whilst its position, adjacent to the crop, will ensure its ability to do as this pattern requires.

Only as the insect leaves the shelter of the vegetation, possibly due to a biological function such as a photo-positive reaction, may control of flight direction be lost and physical factors become predominant.

The control of numbers in the total aerial population is almost entirely a biological phenomenon, except perhaps when insects get into fast moving air, for this may make active alighting difficult, either aerodynamically or through the insects' behaviour, and so may prolong flight.

An example of the different ways in which the same total numbers of aphids may be distributed in the air is given by Johnson (1957*b*) using the data for 8 August 1955. On this occasion the extrapolated density at vegetation level showed a bimodal curve with peaks in the late morning and afternoon. This is typical of the flight of *Aphis fabae* from a crop of beans on many occasion (C. G. Johnson, Taylor & Haine, 1957) and is a common feature of aphid flight in general (Eastop, 1951). The curve for total numbers in the air had the same form, but the morning peak was slightly delayed (fig. 1). The rate of upward

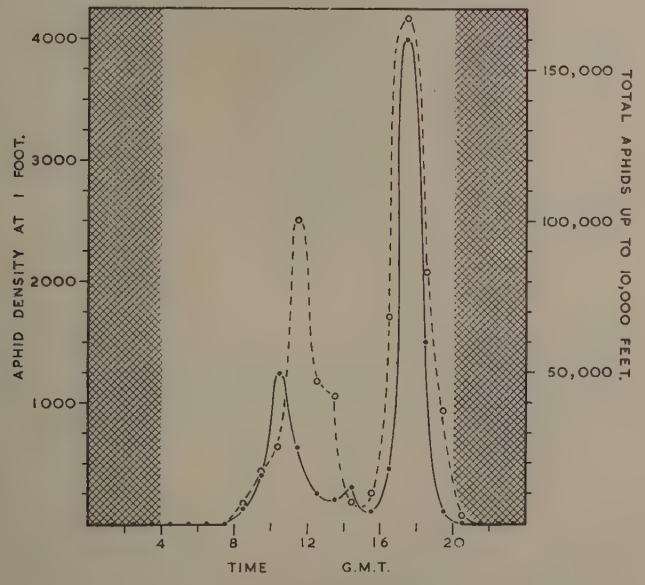

FIG. 1.

——●—— Bimodal curve of aphid density per 10^6 cu. ft. of air at vegetation level estimated from data for 8 August 1955.

– – o – – Total aphid content of a column of air of 10^6 sq. ft. base area from 1 to 10,000 ft., estimated from the same data.

transport was high in the morning and low in the afternoon so that during the first peak the mean height of flight was about 1700 ft. whereas in the second peak it was only 50 ft. These values are typical of the range found in this country and it is rare for the majority to be below 50 ft. except during the first and last hours of flight.

The average duration of flight, estimated from the relative positions in time of the vegetation level and total number curves, is of the order of 1–3 hours in the morning and considerably less in the afternoon. Durst suggested that frictional eddies of up to 50 ft. in diameter and convectional eddies of the order of 1500–2000 ft. in height are to be expected as part of the wind pattern at Cardington (Giblett and others, 1932) and the time taken to circulate up to 2000 ft. and down again is of the order of up to $\frac{1}{2}$–1 hour so that the times and heights given are feasible, provided the aphids in the air are constantly

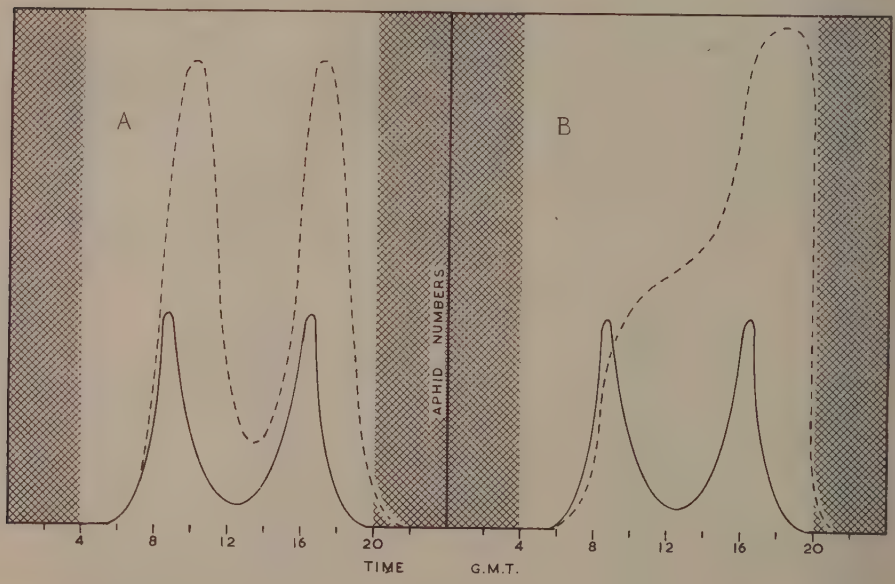

FIG. 2.

———— Bimodal curve for aphid density at crop level based on data for *A. fabae* at Rothamsted 26 July 1948 and 4 July 1949.

– – – – – Expected curve of total numbers in the air based upon the curve at crop level with ; A. 2 hours flight ; B. continuous flight until curtailed by low light intensity (see C. G. Johnson, Taylor & Haine, 1957).

For total numbers the scale of $A = 2B$. Both are arbitrary relative to the crop level density.

changing, those which alight being replaced by others. If the same aphids remained continuously in flight, at any level, the curve for total numbers would not be bimodal (see fig. 2). Also the supply curve from a crop infested with *Aphis fabae* is of aphids taking flight for the first time as their wings dry out (Taylor, 1957). Its' periodic nature depends upon synchronization in the development of flight-immature individuals in the population (C. G. Johnson & Taylor, 1957) and the resulting periodicity would not appear

in a flight-mature population. For the troughs in activity are caused, not by inhibition of flight in flight-mature aphids, but by *lack of available aphids*. Thus the curve for total aerial numbers probably also consists mainly of aphids on first or early flights, for it is of the same type : the aerial population must be very short-lived.

This appears to contrast sharply with the flight pattern of locusts which, even if they settle out of a swarm, take off again to rejoin the others flying overhead so that the same individuals comprise the aerial density throughout the day. Thus the vertical density profile measured hourly in a swarm of locusts, and moving along with it, might be expected to show discontinuities or changes in λ during the day but, irrespective of this, the total numbers in the air would rise at take-off in the morning and remain fairly constant until they fell at settling out in the evening. There are almost always some insects on the ground underneath the swarm (see later) and as a consequence, the density near ground level would be expected to rise to a peak at take-off, fall to a fairly constant low value during the day and could rise to another peak at settling out in the evening if activity persisted after the swarm had stratified.

These differences between the diurnal fluctuations in the aerial statistics for locusts and aphids are apparently caused entirely by the behaviour of the insect and are fundamental to the understanding of the results obtained by trapping. An alate *Aphis fabae* (Scop.) which has not yet flown is persistent in attempting to take off even in most adverse conditions (Müller & Unger, 1951 ; Haine, 1955) and will fly straight up into bright light and. incidentally, into moving air. But this behaviour changes after only a short period, of active flight, of the order of one hour, after which the aphid is willing to settle down on a suitable host plant and commence reproducing (B. Johnson, 1955). The flying life of many species of aphid is definitely limited to a few days by wing muscle autolysis, the onset of which is often stimulated by reproduction (B. Johnson, 1955). Thus the complex of aphid flight behaviour is, in many species, apparently attuned to one or a few short periods of flight and then a long, sedentary reproductive phase.

Locust flight behaviour, on the other hand, is adjusted to a long flying life. Part of this is evident in the gregarious attraction which causes those individuals which alight from the bottom of the swarm to fly up into it again. So a persistent aerial population is maintained and the swarm as a whole moves along, day after day, by the intermittent flight of its individuals. This process has beeen repeatedly observed in locust swarms. In the words of Gunn, Perry, Seymour, Telford, Wright & Yeo (1948, p. 15) " There were, in our experience, always locusts on the ground underneath those in flight, and some were always dropping out to settle while others joined the fliers again ". This is confirmed by Kennedy (1951, Table 2) who gives, out of 53 observations on swarm height, 40 extending down to ground level and amongst the remainder 2 recorded as " part settling ". Rainey & Waloff (1957*b*, Table 1) give 30 observations, all of which extend from ground level upwards, and in more extensive later observations, flying swarms have only very rarely been seen completely clear of the ground (Rainey, personal communication).

The motion of the swarm as a whole is described by Gunn *et al.* (1948, p. 49) ; " All of the swarms we saw progressed in rolling fashion, with some of the locusts always settled below the moving mass ". This rolling motion has been shown by Rainey & Waloff (1951) to conform with what is to be expected from the cellular structure of air movement described by Durst in Giblett and others (1932). The active take-up and deposition of the powerful locust by rising air in the lulls and descending air in the gusts of the larger air cells has been described in detail by Rainey & Waloff (1951) for high flying swarms, and by Kennedy (1951, p. 179) in these words—" it can be stated with some assurance that whenever a low flying swarm was observed in windy weather,

its flight activity (the proportion of insects flying) and its height of flight decreased when the wind rose and increased when it fell ".

Writing now of aphids Kennedy (1950) states that " the number to be seen in flight at a given point rises in lulls and falls in gusts in a strikingly sensitive way " and this is confirmed by Müller & Unger (1952). Thus, although observation of aphid flight is difficult, the impression gained is that the wind structure which has so successfully been used to interpret aerial movement in locust swarms may equally well interpret the movement of aphids. The fact that the locust swarm is almost always in contact with the ground suggests that the circulation of the air will also bring aphids into the still region close to the ground. This would give them the opportunity to alight which their active flight in the wind has apparently conditioned them to accept, and so provide the mechanism necessary to explain the conclusions drawn from the trapping data.

A flight reflex is stimulated in an aphid by moving air ; its initial flight is strongly vertical and its flight attitude is adjusted to this (B. Johnson, 1956) ; take-off persists in winds many times the aphids own flight speed (Haine, 1955) ; flight usually occurs to a large extent during times of air circulation (C. G. Johnson, Haine & Taylor, 1957) : so that there does not appear to be any notable adaptation to avoid wind-directed flight. In fact the majority of aphid migration takes place in windy weather. (C. G. Johnson, 1952) and this may partly account for the relatively large proportion of aphids amongst the insects in the upper air. In aphids the time spent in the air will be largely a function of the time for reversal of flight behaviour and of the opportunity for alighting, in other words of the size of circulation they enter.

Take-off in insects involves problems similar to those of spore release in plants. Spores must cross the thin layer of still air close to the ground before they can enter turbulent air leading into the free circulation necessary for their dispersal (Gregory, 1945). The ejection of spores across this boundary layer, by Ascomycetes for example, is a close parallel to the vertical take-off flight of aphids : both are responses to current climatic factors and both may lead to dispersal dependent upon air movement.

For insects the air layer which must be crossed before free circulation is entered is that in which air movement is less than flight speed or within which the insects sensory mechanisms and behaviour permit active orientation to the ground—whichever is the smaller on any particular occasion. This " boundary " layer may be deep if the air is quiet or the insects' flight is powerful, and then the insects whole flying life may be passed within it. But in a gust of wind the layer may become indefinitely thin and once the boundary layer has been crossed, alighting can only be accomplished after it has been re-entered. This depends, not upon the insect, but upon the movement of the air.

Many insects, other than aphids, enter the circulating air above the boundary layer and once in it they must follow the same pattern of movement to a large extent. The proportion doing so will depend upon their behaviour particularly at and just after take-off ; their flight persistence and power in relation to wind speed ; their sensory mechanisms ; but most of all it will depend upon their diurnal periodicity of flight in relation to the diurnal periodicity of air movement. To try to distinguish between " active " and " passive " migration without considering these features is unlikely to be very profitable.

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ATMOSPHERIC MOVEMENTS AND THE BIOLOGY OF THE DESERT LOCUST (*Schistocerca gregaria* FORSKÅL). By R. C. RAINEY, Desert Locust Survey, East Africa High Commission.

Flying swarms have been observed to vary enormously in height of flight, with the topmost locusts at less than 30 ft. on some occasions, and with locusts all the way up from the ground to more than 5000 ft. above it at other times—with the spacing or density of the flying locusts in them (determined photographically) ranging from more than 10 locusts per cubic yard down to about 1 locust per thousand cubic yards. For studying the part played by atmospheric turbulence in these differences, use has been made of the fact that vertical gradients of air temperature not only greatly influence the intensity of turbulence (as has been illustrated by data on the vertical distribution of airborne aphids), but also determine the height to which such turbulence can extend above the ground, so that the height of the " ceiling ", which is thus imposed on thermal up-currents rising from the ground, is readily found for any particular occasion on which observations of upper-air temperatures are available. The topmost locusts in large, high-flying swarms have been found by this means to be in the

immediate vicinity of the corresponding ceiling imposed on thermal up-currents by the vertical temperature distribution at the time.

Such observations on temperature gradients provide only indirect, circumstantial evidence on the actual air currents concerned. More direct evidence on the strength and distribution of the turbulent air movements encountered by high-flying locusts has been provided by accelerometer, recording the vertical accelerations imparted by these air currents to aircraft transversing them. Such accelerometer records have shown that gliding locusts in the upper parts of high-flying swarms are likely to have encountered up-currents, strong enough to cause them to maintain height without muscular work, at horizontal intervals averaging only a few hundred yards.

The density and distribution of flying locusts in the vertical are thus profoundly affected by the same process of atmospheric turbulence, which is of such importance in the dispersal of spores and pollen, and is so impressively utilized by soaring birds. Turbulence however involves air movements in all directions, lateral as well as vertical, and there is on the other hand good evidence that the behaviour of locust swarms is strikingly opposed to lateral turbulent dispersal. Thus individual flying swarms have been observed to retain their identity for periods of weeks and to travel for hundreds of miles as coherent entities, despite a degree of air turbulence capable of dispersing clouds of inert airborne material of comparable extent within a matter of hours ; such turbulent dispersal was in fact successfully opposed by the active behaviour of the locusts concerned.

Rain is essential for successful breeding by the Desert Locust, which nevertheless occurs most frequently in areas with an average annual rainfall of only 5–10 in.; and Desert Locust swarms, like true nomads, travel in general from areas where the seasonal rains have ended to other areas in which they are beginning. So far, all moving swarms for which adequate evidence is available on direction of displacement and on the corresponding wind (on the spot and at the time), have travelled directly down-wind. Such movement down-wind leads, in general and on balance, from zones of divergence into zones of convergence. Zones of convergence are defined as areas across whose surface boundaries there is a net excess of inflowing air over outflow, and are therefore areas above which air rises ; convergence is an essential factor in the production of widespread heavy rain. The hypothesis that the major displacements of locust swarms take place down-wind, towards and with zones of convergence, has been found capable of accounting not only for the general seasonal pattern of swarm movements between regular breeding areas, but also for each of a number of striking exceptions to these regular movements which have so far been investigated.

Locusts, under the influence of mutual stimulation, are perhaps among the most regularly airborne of insects. Once they are in the air, their subsequent distribution and movement are profoundly influenced by the atmospheric processes of turbulence, operating over distances of hundreds or thousands of feet, and of divergence and convergence, operating over hundreds or thousands of miles ; and the part played by convergent wind flow in the production of rain would appear to confer a substantial survival value on the flight habit in arid regions.

SOME ASPECTS OF FLORAL VASCULAR SYSTEMS.

By K. R. Sporne, The Botany School, Cambridge, England.

(With 8 Text-figures.)

On 7 March, exactly sixty-eight years ago, Henslow (1889) read a paper to this Society " On the vascular systems of floral organs and their importance in the interpretation of the morphology of flowers ". To-day, this topic is no less controversial than it was then. There is still no agreement among morphologists as to the fundamental nature of floral organs, nor even as to whether the course taken by vascular bundles constitutes valid evidence. There are those who uphold the classical view that floral organs are fundamentally leaf-like and those who believe that they are stem-like. Likewise, there are those who regard vascular systems as highly conservative and as a most important guide to phylogeny and there are those who insist that the course taken by vascular bundles can have only slight significance. No attempt will be made here to summarize the evidence which has been brought forward in support of these conflicting views. An extensive review has already been published by Puri (1951).

While it is true that a great amount of work has been done on floral vascular systems, with very few exceptions, published accounts suffer from one great disadvantage, viz. that it is very difficult for the reader to visualize the vascular system as a three-dimensional structure. This arises from the fact that the majority of workers have relied upon serial sections and have then illustrated their descriptions by means of a few selected sections from the microtome ribbon. No doubt the writers of such descriptions have a mental image in three dimensions, but comparatively few attempt to commit it to paper. As examples of what might be done, one could mention the beautiful drawings by Bonner (1948) illustrating the floral vascular system of *Epilobium* and those by his colleague Vautier (1949) of members of the Polygonaceae. Some workers (e.g. Wilson, 1937) have tried to help the reader by means of diagrams of vascular systems supposed to have been opened out flat. However, so long as the work is based on the interpretation of serial sections, progress in the understanding of floral vascular systems is bound to be slow. Those who hope to get a birds'-eye view of the angiosperms must have recourse to more rapid methods of investigation, not only in order to examine the large number of families, genera and species, but also to get some insight into the extent of variation between individuals of one and the same species. Only then will it be possible to assess the extent to which structural differences are of phylogenetic significance.

Clearing techniques have the advantage of rapidity. They have the very great advantage, also, that the vascular system can be observed in its three dimensions directly and that it can be drawn by camera lucida in proper perspective. It is, of course, not suggested that clearing methods should entirely replace the cutting of serial sections, for there are many features of the vascular system which cannot otherwise be studied. Of the various clearing methods which are available, I have found most convenient one which uses lactic acid both for the initial clearing and as a permanent mounting medium (Sporne, 1948). By its use, I have examined, during the past ten years, representatives of some 250 genera belonging to 150 families of dicotyledons. Throughout this work, my concern has been to find evidence which might have some bearing on the problem of the intrinsic nature of the floral organs and I have asked myself the question " Does the vascular system of the receptacle look like a stem system with leaf traces coming from it ? "

To this question Eames has given an answer in the affirmative and to support it he has published (Eames, 1931) reconstructions of the floral vascular systems of many species. That of *Aquilegia* will be familiar to many because it has been reproduced by Eames & MacDaniels (1947) in their text-book. It shows a continuous cylinder of wood from which the traces to the sepals, petals, stamens and carpels depart leaving a gap. However, a cleared flower of *Aquilegia vulgaris* Linn. shows the vascular system to be very different from this, particularly in respect of the stamen supply. Fig. 1 is a drawing made under camera

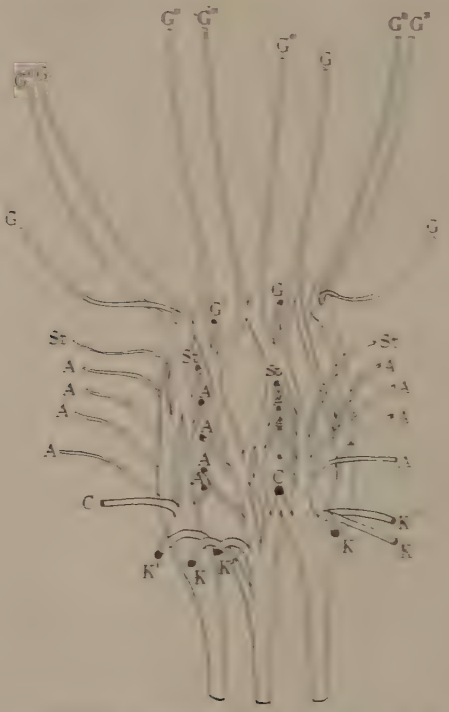

FIG. 1.—*Aquilegia vulgaris* Linn. A thick vertical slice through the receptacle, cleared in lactic acid and viewed from the side.

KEY TO SYMBOLS USED.

K = Sepal supply (*K'* = median, *K''* = lateral).
C = Petal supply (*C'* = median, *C''* = lateral).
A = Stamen bundles.
G = Carpel supply (*G'* = dorsal, *G''* = ventral).
P = Perianth bundles.
St. = Staminode bundles.

lucida of the vascular system as seen in a cleared vertical slice through a flower of this species collected at the stage of anthesis. Instead of a complete cylinder entering the receptacle, there are several separate bundles which branch and recombine in an irregular manner. Three bundles (*K'* & *K''*) enter each sepal and one (*C*) enters each petal. Above these are spaces which could be likened to leaf gaps, except that they are continuous through the stamen region. It is opposite these gaps that the stamens and staminodes lie in vertical rows.

The stamen supply is peculiar in that it is frequently derived from the fusion of two small bundles which have separate origins from opposite sides of the gap. All these features have been noted already in *Aquilegia formosa* Fisch. var. *truncata* by Tepfer (1953), though he figures *all* the stamen-bundles as having this peculiar double origin. Having noted the differences between Eames' reconstruction and his own, Tepfer achieved a reconciliation of the two by suggesting that the differences were due to the different ages at which the flowers were collected. By the time the carpels have started to ripen, cambial activity has laid down secondary wood between the primary bundles in the receptacle so as to produce a continuous cylinder of wood interrupted only by small gaps where the traces depart to the floral organs. These observations are important, not only because they point to the necessity of examining flowers of comparable age, but also because they show that comparisons between floral and vegetative vascular systems must be made either between primary structures in both cases or between secondary structures in both cases. It is probably true that almost all the investigations which have been made so far concern the primary tissues of the flower, since they have been carried out at the stage of anthesis, rather than at a stage when all organs except the carpels have withered and dropped off. Comparisons, then, should be with the primary systems of the stem. Not only must the concept of leaf gaps and leaf traces be examined critically in the flower, it must be examined equally critically in the stem.

The study of primary stem structures was pioneered by Nägeli and occupied the attention of botanists many years ago. Early text-books (e.g. van Tieghem, 1891, and de Bary, 1884) dealt with the matter in some detail, but then this particular aspect of morphology went out of fashion until Dormer (1945) recently revived it. He drew attention to the existence among Leguminosae of two contrasting types of primary stem system which he referred to as "open" and "closed" respectively. As an example of an open system he quoted *Cytisus scoparius* in which there are several longitudinal primary bundles, without any lateral connections, from which the leaf traces come off at regular intervals. The condition in *Cytisus* is thus similar to that described by Scott (1923) for *Lyginopteris*, in both of which the leaf trace is single at its initiation. *Acacia*, *Sophora* and *Sutherlandia* are further examples quoted by Dormer of open systems, but they differ in that each leaf receives three bundles. By contrast, closed vascular systems exhibit lateral connections between adjacent longitudinal bundles, a condition which is found in numerous herbaceous Leguminosae. In those examples figured by Dormer the leaves receive three traces each, but this is not an invariable rule, for van Tieghem figured closed vascular systems in which the leaf traces are solitary. [Incidentally, it is interesting to discover that the mode of origin of the leaf traces in *Cerastium frigidum* (van Tieghem, 1891, fig. 495) is similar to that of the stamen traces in *Aquilegia*. More recently, a somewhat similar twin-origin of the leaf traces has been recorded by Swamy & Bailey (1950) in *Saraca indica* (Chloranthaceae).]

Dormer suggested that lateral connections between adjacent stem bundles may have a physiological importance in providing alternative routes for metabolites. In plants with a cambium, this lateral connection is very soon provided by the secondary wood which is laid down in the interfascicular spaces, but in herbaceous plants any such lateral connections must be by primary strands. He thus explains a correlation between the woody habit and open primary stem systems and a corresponding one between the herbaceous habit and closed primary stem systems. So far as primary structures are concerned, therefore, the student of phylogeny should think in terms of open and closed systems rather than in terms of a cylinder perforated by leaf gaps. The latter is a concept which, although applicable to fern steles, should not be applied to the stems of flowering plants.

We are now in a position to look once more at the primary vascular systems of flowers and to compare them in this new light with primary stem systems. It is proposed here to restrict the scope of the investigation to include only flowers with many stamens, assuming that such flowers are relatively primitive and are, therefore, more likely to give some hint as to the fundamental nature of the stamen than would more advanced flowers. A further restriction is to exclude flowers with inferior ovaries.

The primary vascular system of the flower of *Trollius europaeus* Linn. is illustrated in fig. 2. A number of discrete bundles enter the receptacle from the

FIG. 2.—*Trollius europaeus* Linn. Perspective drawing of a half-flower made transparent with lactic acid. Details in the centre of the drawing are accurate, but those at the sides are merely sketched lightly. (The floral organs have been removed.)

peduncle, but these anastomose before the perianth- and the nectary-bundles are given off. At this level, therefore, the system could be described as "closed". However, above this level there are many longitudinal bundles which have only occasional haphazard interconnections and from which the stamen-bundles arise in succession. In some places a stamen-bundle arises at a point of interconnection in a manner comparable with that of a leaf trace from the dictyostele of a fern, but this is the exception rather than the rule. Lateral connections are even rarer in *Clematis douglasii* Hook. (fig. 3), where the vascular system could be described as "open" above the level of the perianth members. *Anemone japonica* Sieb. & Zucc. (Fig. 4) has a rather more complex vascular system in that there are two coaxial systems in the peduncle. These coalesce into a single

cylinder which, at the level of the perianth, is " closed ". What may be the significance of these observations it is hard to say, but one is tempted to argue that, since the life of the stamens is short compared with that of the carpels the stamen vascular supply need not be so efficient. Whether this be the correct interpretation or not, it is incidental to the main problem of the nature of the stamen. In the four genera described so far, all of which are members of the Ranunculaceae, there is nothing to suggest that the vascular supply to stamens is fundamentally different from that of leaves (provided that all thought of cylinders perforated by leaf gaps is abandoned).

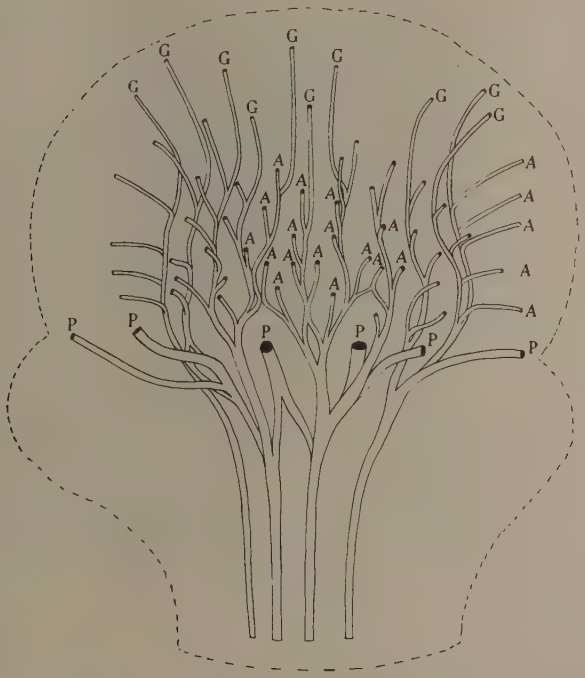

FIG. 3.—*Clematis douglasii* Hook. A thick vertical slice through the receptacle, viewed from the side.

Twenty years ago, however, Wilson (1937) claimed to have found evidence to the contrary. He had noticed that, in some families of dicotyledons, groups of stamens received their vascular supply from a common trunk bundle which branched many times in a tree-like fashion within the receptacle of the flower. *Hibbertia scandens* Dryand. (Dilleniaceae) (fig. 5) provides a good example of this kind of flower. The figure was drawn looking down from above into a thick horizontal slice through the receptacle of the flower at the level of the stamens. Many trunk bundles are visible (actually thirteen, though the number is insignificant, since it would be fewer if the slice had been lower in the receptacle, by reason of the fusions which occur lower down) and these branch many times in giving rise to the large number of stamen-bundles. *Hypericum patulum*

Thunb. (Guttiferae or Hypericaceae) (fig. 6) is similar, except that the number of trunk bundles is fixed in relation to the number of stamen fascicles.

Such " dendroid " stamen supplies were held by Wilson to support the belief that stamens represent the ultimate tips of branching stem-like structures, relics of which still survive in the branching vascular bundles supplying them. Other families which Wilson listed as showing this particular feature are Crossosomataceae, Ochnaceae, Cochlospermaceae, Bixaceae, Bombacaceae and Malvaceae.

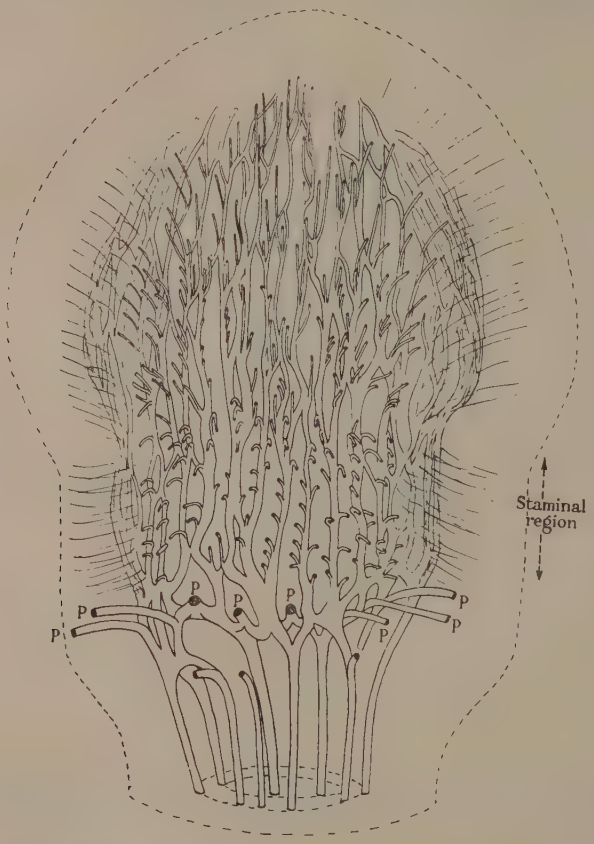

FIG. 4.—*Anemone japonica* Sieb. & Zucc. Perspective drawing of a half-flower. (The floral organs have been removed.)

To this list I would add the families Aizoaceae (or Ficoidaceae), Loasaceae, Flacourtiaceae, Theaceae, Lecythidaceae, Actinidiaceae, Tiliaceae and the genus *Paeonia* (now removed by some taxonomists from the Ranunculaceae and placed in Paeoniaceae). Fig. 7 was drawn from a portion of the receptacle of *Mesembryanthemum lehmanii* Eckl. & Zeyh. (Aizoaceae) viewed from within. The carpellary tissue and its vascular supply have been dissected away, while the remaining tissue has been opened out flat. The vascular bundles which are drawn in outline represent the supply to the perianth

members and to the receptacular tissue beneath them. The bundles which are shown in black supply the stamens and the many petaloid staminodes (described by some as petals). They are much branched and, were it not for the occasional anastomoses which occur, they would bear a close resemblance to fruit trees trained against a wall. Similar branching vascular bundles were figured by Sporne (1948) for *Sparmannia africana* L. (Tiliaceae) in which the stamens receive all their vascular supply from eight trunk bundles. Fig. 8 was drawn from a horizontal slice through the flower of *Paeonia arietina* Anders. The perianth supply is shown in outline, while the stamen supply is shown in black.

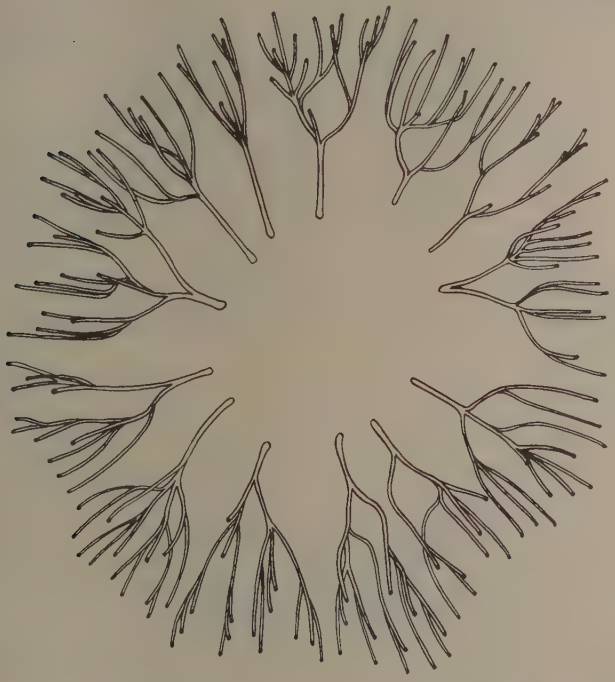

FIG. 5.—*Hibbertia scandens* Dryand. Staminal vascular supply, seen from above, in a thick horizontal slice through the receptacle.

The latter is seen to be derived from an indefinite number of trunk bundles and is more complex than those described so far, in that there are numerous anastomoses.

Corner (1946) did not agree with Wilson's claim that dendroid stamen supplies give evidence of an ancestral branching stamen, but instead suggested that they are correlated with a reversal of the normal sequence of initiation of stamen primodia. He showed that the stamens of members of the Bixaceae arise in centrifugal sequence and drew attention to the same phenomenon in *Paeonia*, in many of the families listed by Wilson as having a dendroid stamen supply and in all the additional families mentioned above by me. In the light of these observations, it is not difficult to reconcile the two contrasting types of vascular system exemplified by *Clematis* and *Hibbertia*. In *Clematis* branching bundles can be seen growing, as it were, towards the apex of the flower (following

the centripetal origin of the stamens), while in *Hibbertia* there are branching bundles "growing" away from the apex of the flower (following the centrifugal origin of the stamens). *Trollius* and *Paeonia* provide another contrasting pair. In both vascular systems there are anastomoses which would justify the description "partially closed", but one is centripetal while the other is centrifugal. Corner suggested that the centrifugal condition must have been derived from the more usual centripetal state. Thus, it would follow that, among polyandrous

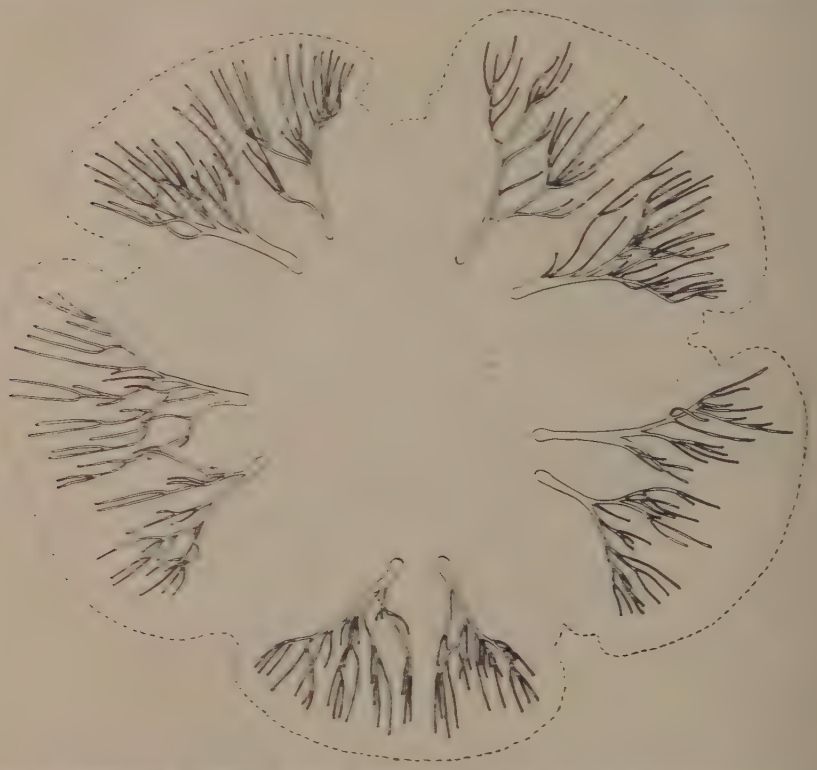

FIG. 6.—*Hypericum pseudum* Thunb. Vascular supply to the five stamen fascicles, seen from above, in a thick horizontal slice through the receptacle.

families, those listed by Wilson as showing relics of an ancestral condition are, on the contrary, relatively advanced.

We are led to the conclusion that, in so far as vascular structures tell us anything at all of evolutionary processes, they do not suggest any intrinsic difference between stamens and leaves. To this extent, therefore, the classical theory is upheld; but it does not follow that stamens have evolved from leaves any more than that leaves have evolved from stamens! A much more acceptable interpretation of their intrinsic similarity is to suppose that both stamens and leaves have evolved from some common origin along quite different lines. What this hypothetical common origin might have been must, for the moment, remain a matter for speculation, but there is certainly no justification for

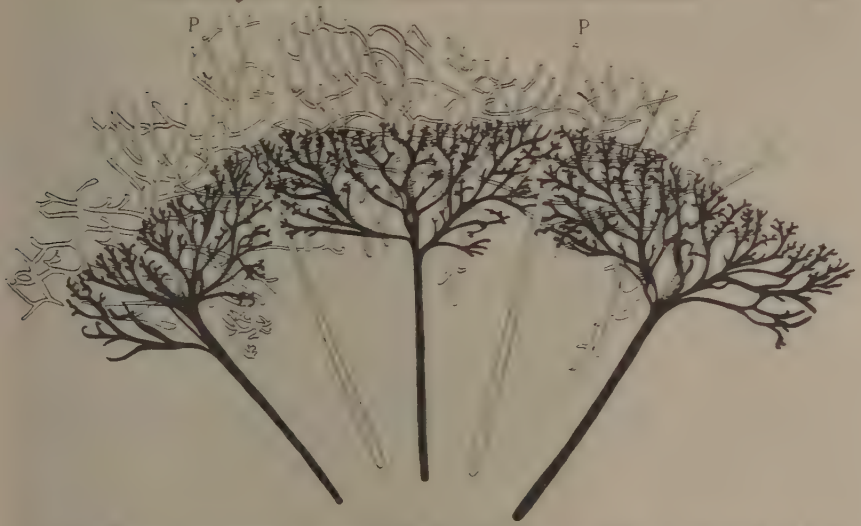

FIG. 7.—*Mesembryanthemum lehmanni* Eckl. & Zeyh. A portion of the receptacle, laid out flat and viewed from within after the carpellary tissue had been dissected away. Vascular bundles drawn in outline supply the perianth members and the receptacular tissue. Those in black supply the stamens and staminodes.

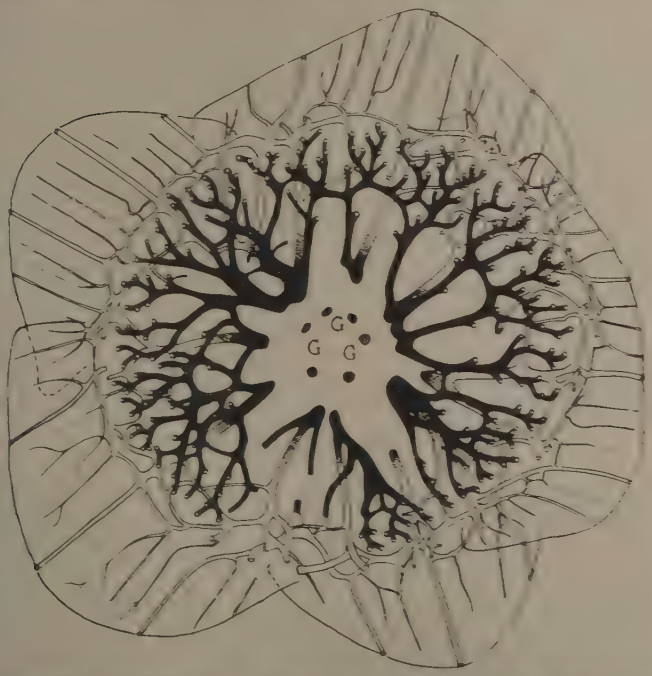

FIG. 8.—*Paeonia arietina* Anders. A thick horizontal slice through the receptacle, viewed from above. Vascular bundles drawn in outline supply the perianth members. Those in black supply the stamens.

assuming it to have been a fertile foliage leaf such as the term "sporophyll" implies.

Summary.

A plea is made for a wider use of clearing techniques in studying floral vascular systems.

Most investigators concern themselves with the primary vascular system of the flower. Comparisons should, therefore, be with the primary system of the stem in order to discover any evidence of intrinsic similarity between floral organs and leaves. The primary vascular systems of both can be interpreted as "open" or "closed", but not in terms of leaf gaps and leaf traces as in dictyostelic ferns.

Not only does this apply to flowers in which the stamens arise in centripetal succession (e.g. Ranunculaceae), but also to those in which they arise in centrifugal succession (e.g. Dilleniaceae, Tiliaceae, Paeoniaceae, in which branching vascular bundles supplying the stamens have previously been claimed as relics of an ancestral branch-like stamen). Stamens and leaves are, therefore, held to be homologous.

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SYMPOSIUM ON PLANT-PARASITIC NEMATODA*

Introduction. By B. G. Peters.

More than 100 species of nematodes have become adapted to a life of more or less close association with plants. Such a mode of life appears to have been evolved independently in two very different suborders of soil-inhabiting nematodes: the Tylenchina and the Dorylaimina, and to have been facilitated in each case by the development of an analogous (but not strictly homologous) organ: the mouth stylet. In structure and function this operates rather like a hypodermic needle, exsertable through the terminal mouth, and with a muscular oesophagus subserving the rôle of the syringe. Plant cells are thus punctured and their fluid contents withdrawn.

* See *Nature, Lond.* (1957), **179**, 902, for further account.

Such associations vary from nematode species living free in the soil but feeding on plant roots from the outside, to species which are obligatory internal parasites. Each species has a restricted range of plant hosts, and also a preferred location in the plant: root, stem, leaf, or inflorescence. In size most adult parasites lie within the length-range 0·5 to 4 mm. In shape, most are vermiform but, in some species from various families, the females become distended and often retain their eggs *in utero* instead of laying them.

Under agronomic systems involving over-cropping or monoculture, a given parasite may increase in numbers to such a level that crop-yields are seriously reduced and the plant may even be killed. Thus, the complex inter-relationships of host and parasite are matters not only of academic interest but also of economic importance. The present symposium touches upon three aspects of such inter-relationships, as exemplified in the genera *Heterodera* and *Aphelenchoides*.

In the dozen or so species of *Heterodera* the young worm is wholly endoparasitic in plant roots but the expanding body of the female bursts out from the cortex, leaving only a narrow neck within for feeding and attachment. She finally becomes lemon-shaped or spherical and her outer covering becomes tanned from a transparent cuticle to a brown leathery substance. She dies and falls off into the soil having become a protective "cyst" full of living eggs. In some species these eggs hatch only sparingly over a number of years, unless stimulated by a chemical substance diffusing in high dilution from the growing roots of a host plant.

Such species of *Heterodera* lend themselves to quantitative estimations of population density, for the cysts can be floated from air-dried soil and counted; the contained larvae can be stimulated to hatch from the egg shells, and to emerge from the cyst, when they also can be counted. The population density of a given species of *Heterodera* in a given soil can thus be estimated with a calculable precision in terms of larvae (i.e., potential adults) per gramme of soil. Moreover, clean soil can be artificially inoculated with parasites at a series of known densities, host plants can then be grown, and the effects on the plant or on the ultimate parasite density can be investigated.

The first of the following papers discusses some experiments of this kind carried out at Rothamsted (Mr. Hesling) and Imperial College (Mr. Hague), using species of *Heterodera*.

The second paper is also concerned with quantitative investigations on a species of *Heterodera* (*H. rostochiensis* Wollenweber, the potato root eelworm), but this time from the aspect of resistance. The resistance shown by a species or variety of host to a given nematode parasite may be only partial: infestive larvae may be able to penetrate into the roots and feed there, but few or none may become functionally adult. As before, effects on the host plant and on the resultant parasite density can be estimated. Experiments at the Cambridge School of Agriculture (Mr. Williams) have been specially concerned with current attempts to breed varieties of potatoes resistant to this, the most serious plant eelworm in Britain.

The third paper deals with a very different type of eelworm, leaf eelworms of the genus *Aphelenchoides*, and a different type of host-parasite situation. These worms remain transparent and vermiform. They can be sometimes ectoparasitic, lying (for example) between the folded leaves in a bud and feeding through the leaf epidermis, and later entering the leaf through a stoma to become endoparasitic. The interesting and unusual situation, studied at East Malling by Dr. Crosse and Dr. Pitcher, concerns a disease complex of strawberry plants in which both the leaf eelworm and a plant-parasitic bacterium are jointly implicated.

Population Studies on Cyst-forming Nematodes of the Genus *Heterodera*.

By N. G. Hague and J. J. Hesling.

(With 7 Text-figures.)

The estimation of the number of individuals which comprise a given population of eelworms may be used to measure the effect on the eelworm of treatments which may be biological, chemical or physical. Such treatments may include the use of different host plants, the application of chemicals, or changes in soil moisture. *Heterodera* populations in the field, however, are also influenced by uncontrollable factors, such as the soil flora and fauna, soil fertility etc. These factors may act directly or indirectly; for example predatory organisms may directly destroy eelworm eggs and larvae, but soil fertility indirectly may effect the nematode because it influences the growth of the host plant.

The population density of the eelworm can itself affect the population dynamics. It has been shown by earlier workers [Chitwood & Feldmesser (1948); Fenwick & Reid (1953); Goffart (1952); Schmidt (1954)] that low initial levels of infestation favour high rates of eelworm increase or vice versa. This has often been overlooked. Knowledge of the influence of the initial level of population on the final level may therefore help in making a truer assessment of experimental results.

The experiments described here were principally concerned with the investigation of the effects on population dynamics of varying the initial population density of two species of *Heterodera*, namely *H. rostochiensis* the potato-root eelworm, and *H. major* the cereal-root eelworm.

For this purpose some of the host plants of these two species were grown in suitably sized pots of soil to which the eelworm inoculum was added in the form of cysts, which are the bodies of mature female worms containing a large number of eelworm larvae enclosed in an egg " shell " or membrane.

The eelworm inocula for both species, which are shown in Table I, were so arranged that the plants were subjected to eelworm infestation levels forming a geometric series.

Table I.—Inoculation rates in terms of larvae per gram of soil.

H. rostochiensis (1954). Replication × 3.
12·25; 24·5; 49; 98; 196; 392; 784.

H. major (1954). Replication × 2.
0·19; 0·38; 0·75; 1·5; 3·0; 6·05; 12·1; 24·2.

H. rostochiensis (1955). Replication × 2.
0·24; 0·96; 3·83; 15·3; 61·3; 245·2.

The cysts used as inoculum were produced in the year before the experiment took place and were considered to be full of eggs. In order to reduce the variability of their content, the cysts were of about the same size, the size selection being achieved by sieving. Cysts of *H. rostochiensis* were handled in the air-dry state, but those of *H. major* were kept moist and at a low temperature (2° C.) during their collection and counting. The techniques used for the collection and handling of cysts and the estimation of their egg content were based on those of Fenwick (1940), Bijloo (1954), and Hesling (1952 and 1956).

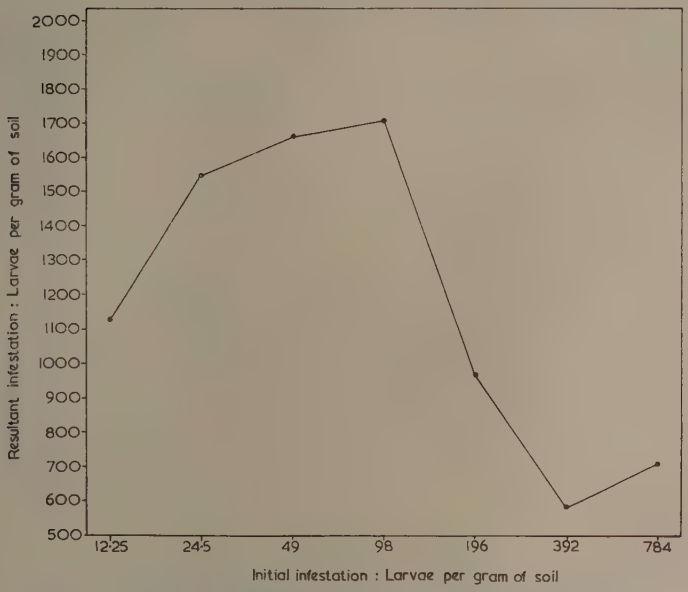

FIG. 1*a*.—*Heterodera rostochiensis* on potato, 1954. The effect of the initial level of infestation on the final eelworm population.

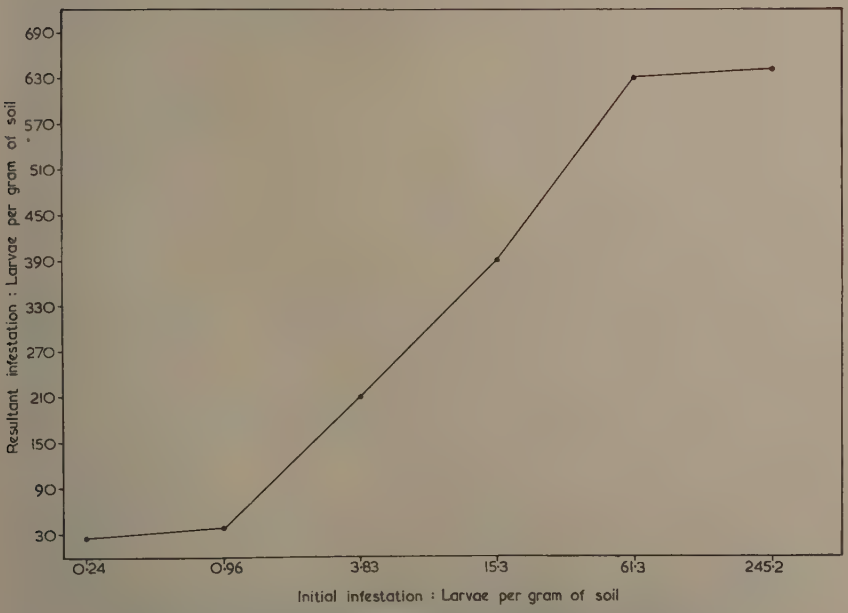

FIG. 1*b*.—*Heterodera rostochiensis* on potato, 1955. The effect of the initial level of infestation on the final eelworm population.

The effect of the initial infestation of the final population was considered in several ways. Comparisons were made between the size of the final populations produced from several different initial levels of infestation, and the relationships between the initial infestation and the eelworm increase and the egg content of the new cysts were investigated.

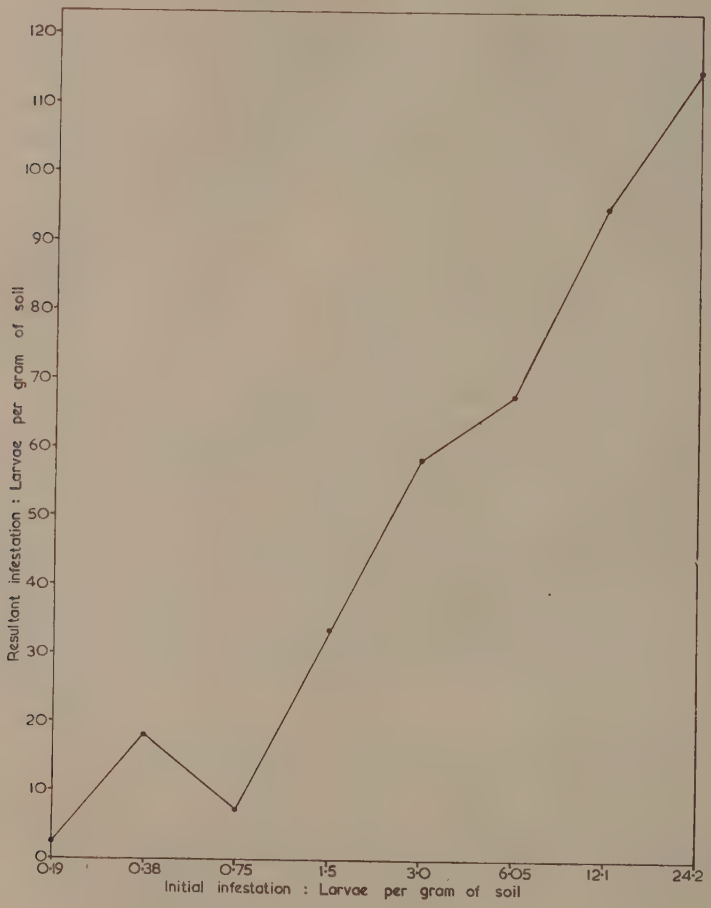

Fig. 2.—*Heterodera major* on barley, 1954. The effect of the initial level of infestation on the final eelworm population.

Results.

Fig. 1*a*, 1*b* and 2 show the form of the curve obtained when the final population is plotted against the original infestation level from which it was derived. It will be seen that the final eelworm population at first rises with increase of the initial infestation. In fig. 1*a* the curve for the 1954 results shows that the final eelworm population appears to have a maximum value under the conditions provided ; beyond the maximum the curve falls. In fig. 1*b* the results indicate that the final eelworm population approaches a maximum at an initial infestation

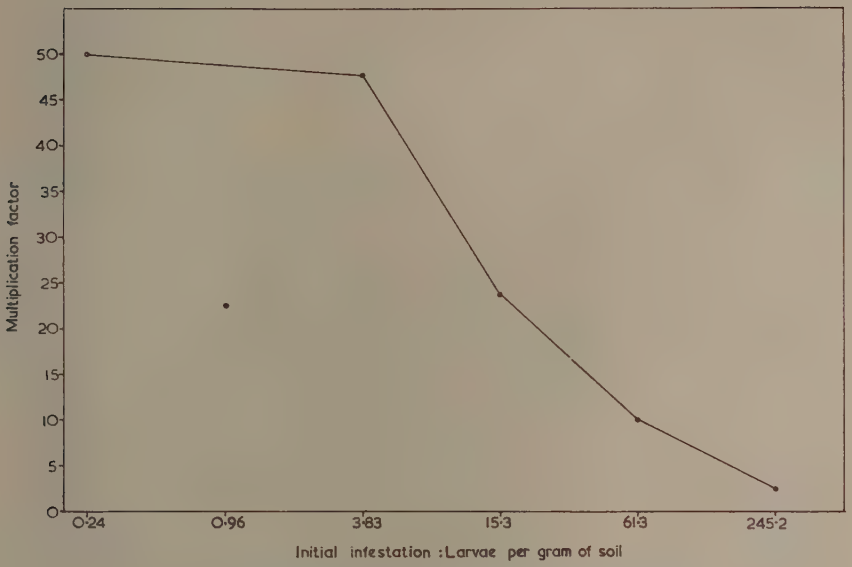

FIG. 3.—The effect of increasing initial levels of infestation on the multiplication factor for *H. rostochiensis*, 1955.

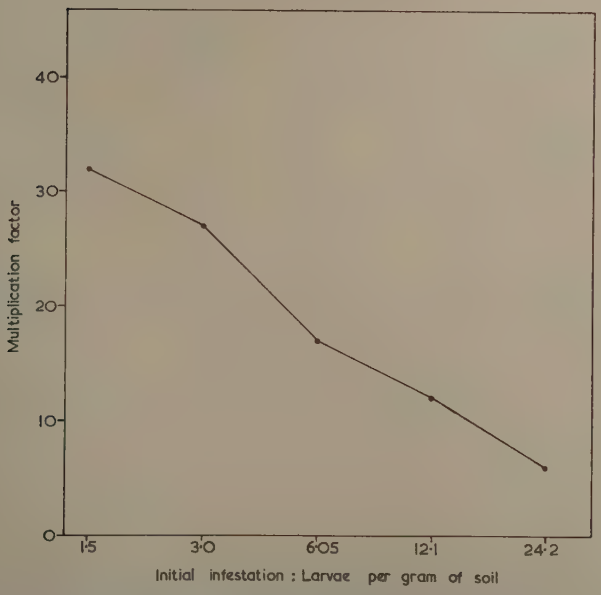

FIG. 4.—The effect of increasing initial levels of infestation on the multiplication factor for *H. major*, 1954.

in the same range as that in 1954. Thus we get an overall picture for *H. rostochiensis* which shows that, as the initial infestation increases, the final eelworm population increases to a maximum with a subsequent fall, the latter probably indicating that at high levels of infestation the injury to the plant is preventing eelworm increase.

In figs. 3 and 4 the multiplication factors for the two species of eelworm are plotted against their initial infestation levels; the eelworm multiplication factor being simply the ratio of the final eelworm population to initial eelworm population from which it was derived, the eelworm units beings eggs per gram of soil. For both species of *Heterodera*, the eelworm increase is largest when the initial infestation is low.

The total final cysts produced from each pot were sieved into four size grades, and the number of new cysts in each grade was calculated as a percentage of the total final cyst population. Figs. 5 and 6 show that the percentage of large cysts is highest at low inoculum levels, while at high inoculum levels there is a larger proportion of small cysts. This effect on the final cyst population is to reduce the mean size of the new cysts as the infestation level is increased. Diminution of the mean cyst size must affect the mean egg content of the new cysts which also falls with increase of the initial inoculum. In the case of *H. major* new cysts of the *same size grade* had the same egg content, irrespective of the size of the initial infestation from which they were derived, but for *H. rostochiensis* (where some of the initial infestations were very high) the number of eggs per new cyst, in the case of the largest new cysts, appeared to decrease at the highest infestation levels (see Table II). Fig. 6 shows that for *H. major* relatively more large cysts per pot are produced on barley than on oats.

TABLE II.—Showing the mean number* of eggs per cyst produced from different initial infestations of *H. rostochiensis*.

Initial infestation levels (eggs/gram soil)	Cyst size		
	> 599 μ	422–295 μ (eggs per cyst)	< 295 μ
12·25	678	119	32
24·5	711	151	61
49·0	642	132	48
98·0	665	152	55
196·0	495	147	42
392·0	228	158	56
784·0	222	162	33

* Derived from 3 replicated batches of 100 cysts.

DISCUSSION.

The relationship between the eelworm and the plant is very complex, it is alterable, and perhaps constantly altering throughout the life of the host plant. It is clear from the experiments described above, that the size of the eelworm infestation is a factor affecting this relationship.

A plant injured by eelworms is probably more susceptible to other pathogens or adverse environmental conditions and this increased susceptibility may be reflected in the size of the final eelworm populations because unhealthy plants generally support fewer eelworms.

Without the effect of other pathogens etc., the changes in the eelworm population at high infestation levels may be only small and so make the clear demonstration of treatment differences more difficult. Thus it seems unwise to use infestation levels in experiments where eelworm population increase and/or eelworm numbers are to be used as criteria for the assessment of experimental results. It is desirable to know the initial level of infestation best suited to the experimental conditions and the form of the curve of the final infestation

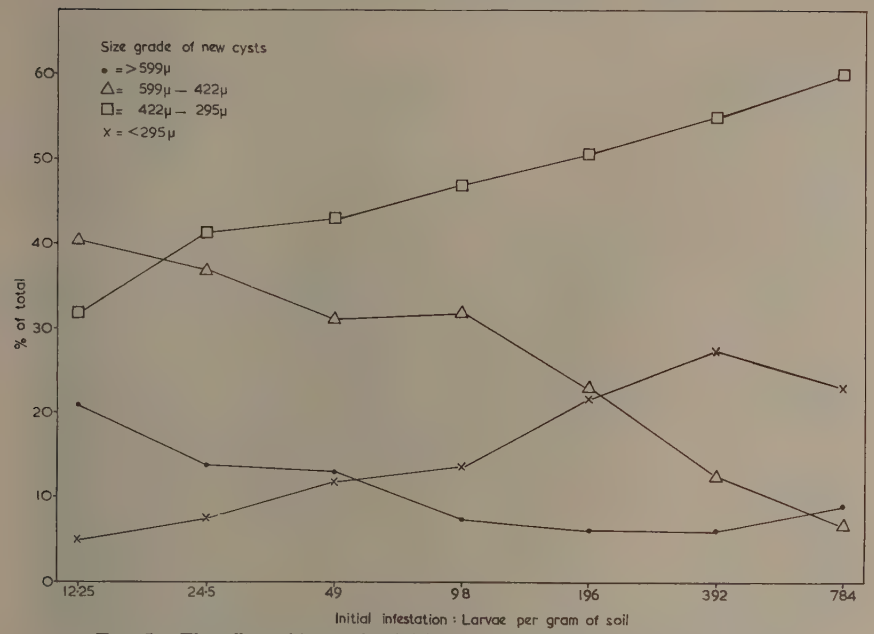

FIG. 5.—The effect of increasing initial levels of infestation of *H. rostochiensis* on the percentage of cysts of different size grades.

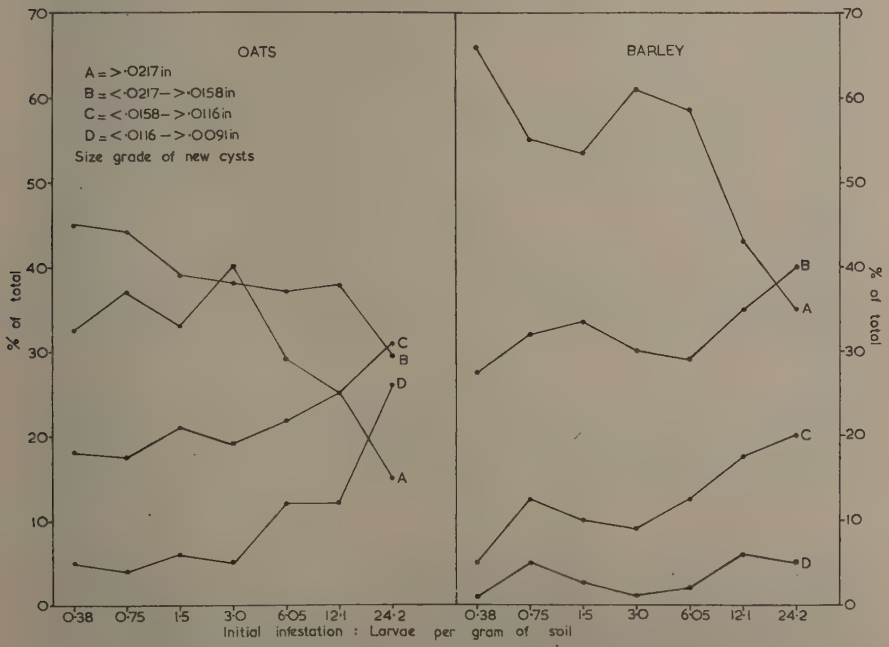

FIG. 6.—The effect of increasing initial levels of infestation of *H. major* on the percentage of cysts of different size grades.

plotted against the initial infestation should be found for the eelworm being studied. For *H. rostochiensis*, the curve (fig. 1*a*) reaches a maximum and then falls, thus there are many pairs of initial infestation levels which may produce the same final eelworm population if the initial population is measured in viable larvae per gram of soil. In order to avoid ambiguity, initial infestation levels lower than those which will give rise to the maximum final eelworm population should be used. The curve in fig. 1*a* refers only to *H. rostochiensis* and it is possible that curves for other species of *Heterodera* may be of a different form. The criterion of increase of population would be particularly difficult to use in a species where the curve fell off sharply after the maximum.

In the above experiments some of the infestation levels were quite low. Investigations into eelworm behaviour at low infestations (e.g. 5 larvae per gram of soil) are rendered difficult because of difficulties of technique and statistical considerations. The soil to which the eelworm cysts are added must originally be eelworm free ; sterilized soil is unsuitable because cysts contained in it will not be removed and they may thus confuse the final eelworm estimations. *Heterodera* populations in the form of cysts are infestations of eelworms in " packets ", since each cyst is a unit containing eggs and larvae. In spite of careful selection of cysts, there is always some variability in the cyst content, not only in the actual number of eggs and larvae per cyst but also in their behaviour. For example the larvae may not mature equally, may not be equally responsive to a hatching stimulus if it is present, or may not be equally capable of entering and developing in the roots of a host plant. Further, at very low infestations, isolated females may not be fertilized. Thus, to offset the effect of variability at low infestations, many-fold replication is required.

The addition to the soil of accurately counted out eggs and/or larvae is an alternative method of setting up low initial infestations. However " free " eggs and larvae may not behave as do those within cysts added to the soil, and the techniques for obtaining, handling and counting these free eggs and larvae are not so well worked out and tested for *Heterodera* as are the infestation methods utilizing cysts.

It has been shown above that a higher proportion of small cysts were produced on plants subjected to high initial infestations with a consequent reduction in the *mean* egg content of cysts produced on such plants. For example, 100 cysts produced from a low initial infestation in a pot might have a mean egg content of 200 eggs, while 1000 cysts produced from a high infestation in a pot might have a mean content of only 100 eggs. These two populations may be expressed as 100 or 1000 " viable " cysts (i.e. containing viable eggs or larvae) per pot. Viable cyst counts would show that one pot held 10 times the infestation of the other, while the factor would be five if the population was measured in larvae per gram of soil, which is in fact the fundamental unit. Therefore cyst numbers alone should not be used in experimental work to express the size of a population or its increase factor.

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Potatoes Resistant to Root Eelworm.

By T. D. Williams, School of Agriculture, University of Cambridge.

(With 7 Text-figures)

Introduction.

The potato root eelworm, *Heterodera rostochiensis* Woll. was first described by Kühn in 1881 as a potato-attacking strain of the plant-parasitic nematode, *Heterodera schachtii* Schmidt. Its importance as a parasite was not, however, fully appreciated until 1914. Since then, intensive potato growing has led to great increases in the extent of infestations, all established commercial varieties being efficient hosts. It is now widely distributed in Europe, and is known to occur in Israel, Algeria, Long Island, U.S.A., Peru and Bolivia. Chemical control measures are seldom economic. This paper describes some of the investigations made at Cambridge into the possible use of eelworm-resistant potato plants as a biological means of control.

Life History of H. rostochiensis.

The life history is similar to the other described species of the genus *Heterodera* (Franklin, 1951).

When soil from an infested field is dried at air temperature, shaken with water and the resulting "float" is examined, small, spherical " cysts "—the dead bodies of the mature females—are found. Within the cysts are the eggs containing coiled larvae. These larvae when fully extended have an average length of 450 μ and possess a protrusible mouth structure, the stylet.

When potatoes are grown in infested soil, the larvae hatch from the eggs, leave the cysts and enter the roots of the plant. Larval hatch is stimulated by an as yet unidentified " hatching factor " produced by the roots of the host. There are four moults during development ; the first moult occurs in the egg prior to hatching, the remainder taking place in the root. During its life in the root, the developing larva feeds on a syncitial complex of cells—the " giant cells "—which form in the vicinity of its head. These cells develop near the vascular tissue, just within the endodermis, and may spread extensively along the central cylinder and often into the cortex. The phloem elements in particular are compressed or completely occluded.

Though the sex of the larvae is not easily discernible during the earliest stages of development, marked sexual dimorphism appears as they approach maturity. The males usually mature some three to four weeks after larval entry, retaining the worm-like form of the larvae but increasing in length to about 1100 μ. Mature females become spherical and may attain diameters of 600–700 μ. Their egg content varies considerably with final cyst size ; some of the largest females may contain as many as 800–900 eggs. During female development, which usually takes about six weeks, the body wall, at first transparent, becomes opalescent, then for a short period bright yellow, finally turning brown. The males leave the root when mature and cluster round the females which protrude from the root as they increase in size.

The Source of Resistant Potato Breeding Material.

The Commonwealth Potato Collection gathered in Central and South America during 1938–39 was the first source of eelworm-resistant plants. Dr. Ellenby, at Newcastle, began in 1941, the task of establishing whether any of the plants collected were resistant, the criterion of resistance being the absence

of cysts on the roots of plants growing in infested soil. In all some 1300 forms were tested (Ellenby, 1954). The most important of the eight resistant lines are shown in Table I. (Modified from Jones, 1954.)

TABLE I.—Lines of potatoes used in breeding for eelworm resistance.

(*a*) Tuberosa. Cultivated.	*Solanum tuberosum* sub. sp. *andigena* (2*n* = 48).	
H1 = C.P.C. 1692	Collected Cochabamba, Bolivia.	
H2 = C.P.C. 1690	,, Puno, Peru.	
H3 = C.P.C. 1685	,, Juli, Peru.	
H4 = C.P.C. 1673	,, La Paz, Bolivia.	
(H1, H2, etc., designations used at the Plant Breeding Institute, Trumpington.)		
(*b*) Tuberosa. Wild.	*Solanum vernei* (2*n* = 24).	
C.P.C. 2413.1		
C.P.C. 2414.3		

Solanum tuberosum sub. sp. *andigena* (Juz & Buk.) Hawkes, (hereafter referred to as *S. andigena*), is the ancestral form of *S. tuberosum* sub. sp. *tuberosum* (hereafter *S. tuberosum*), the cultivated European potato (Hawkes, 1956). Both being closely related tetraploid forms, crossing them presents no especial difficulty.

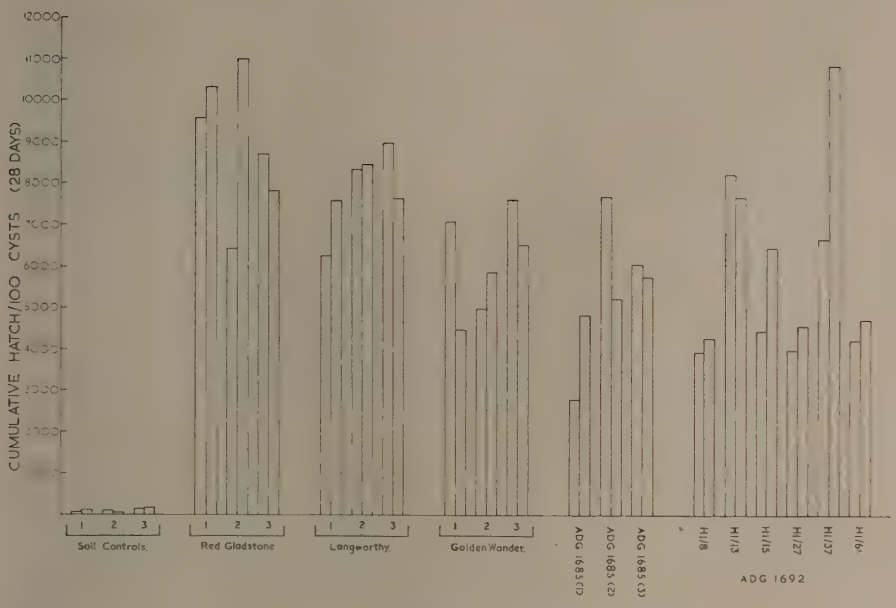
It was appreciated that a combination of the qualities of commercial *S. tuberosum* varieties with the factor suppressing the maturation of female eelworms present in *S. andigena* could be of great value in eelworm-infested localities. Eelworm resistance is not known in existing European varieties: either it was never introduced to Europe, or it was lost in the early stages of selection and improvement.

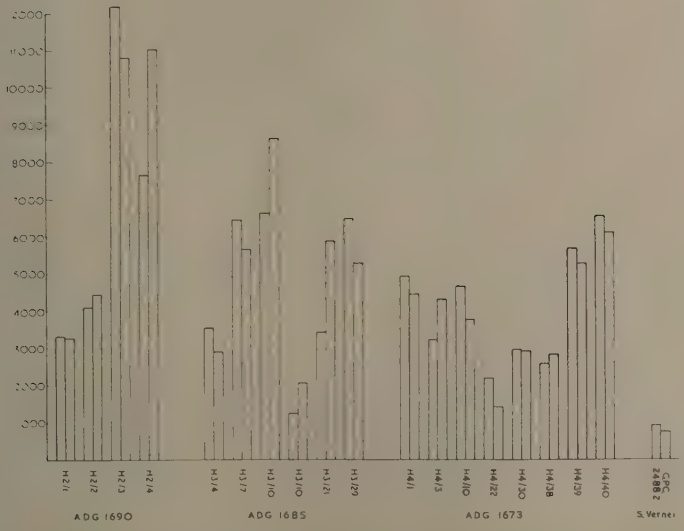
Breeding programmes based on the Commonwealth Potato Collection material began first in Holland in 1951, and one year later at Cambridge and Edinburgh. The Cambridge work was begun by Dr. H. W. Howard of the Plant Breeding Institute, and Mr. F. G. W. Jones of the School of Agriculture. All these programmes have developed similarly, beginning with selted seed of the clones previously listed (Table I). Cambridge breeding has been based mainly on C.P.C. 1690 while in Holland C.P.C. 1673 and 1685 material has been chiefly used. The factor conferring resistance has been designated "H" and is a dominant gene. Similar segregation patterns for this gene have been observed at all the breeding stations and they are in agreement with the theory of tetrasomic inheritance (Toxopeus & Huijsman, 1953; Jones, 1954; Huijsman, 1955, 1957).

All the programmes have reached at least the third back-cross stage, although two back-crosses may suffice to produce the starting material for breeding an acceptable commercial variety if the progeny from the first *S. andigena*—*S. tuberosum* cross is selected for good field characters. Fortunately there is no tendency for the gene for resistance to be linked with undesirable characters e.g. high yield only under short day conditions, though its expression i.e. the degree of resistance, may be somewhat modified by the gene complex in which it occurs. Field selection of progenies provides a number of plants in which resistant and susceptible types occur in the predicted proportions. This greatly reduces the number of plants to be tested in infested soil.

Production of the Hatching Factor by Resistant Plants.

The first series of experiments was made to estimate the hatching activity of root diffusates taken from resistant plants. When controlled amounts of water are allowed to drain through pots of soil in which susceptible potato plants are growing, the resulting leachings have a marked stimulatory effect on





FIGS. 1 and 2.—The hatching activity of root diffusates from resistant *S. andigena* and *S. vernei* plants compared with diffusates from susceptible varieties.

the rate of larval emergence from cysts. Leachings collected in the same way from pots of soil in which no potatoes are growing have no such stimulatory effect. This effect is measured by counting the number of larvae emerging from replicate batches of cysts immersed in 1 ml. of the leachings. The hatching occurs in solid watchglasses, "spent" diffusate is replaced at weekly intervals, counts of emerged larvae being made at these times. The results of the weekly counts are added over a period, usually or three or four weeks, and the final "cumulative" hatch is used as an index of root diffusate activity. The hatching tests (Fenwick, 1955) are conducted at a constant temperature of 24° C., the optimum for larval emergence under these conditions.

Figs 1 and 2 are the results in histogram form obtained by exposing duplicate batches of 100 cysts to the action of root diffusates taken under similar conditions from a range of susceptible and resistant plants. They show that in most cases, diffusates taken from eelworm resistant plants have a high hatching activity. Root diffusates from a clone of *S. vernei* C.P.C. 2488.2 however caused little hatching. Later tests on *S. vernei* material have confirmed the low activity of diffusate taken from several clones of this species.

The Larval Invasion of Resistant Potatoes.

The next step was to find out if any larvae entered the roots of resistant plants, and if so, whether or not further development occurred.

By macerating roots for 20 secs. in an M.S.E. "Atomix" assembly, after staining them in boiling acid-fuchsin lactophenol (Goodey, 1957), the number of any larval stages present can be estimated. This method was used to examine the root systems of resistant plants, taken at intervals from pots of infested soil.

Fig. 3 shows the results of this experiment. Resistant *S. andigena* plants were grown singly in pots containing eelworm infested soil having an estimated content of 280 eggs/g. air-dried soil. Five plants were lifted on each of the sampling dates shown. The times of lifting are given as the number of days following the appearance of the first shoot at soil level to avoid possible errors introduced by delayed sprouting. Each point plotted represents the mean of larval counts for 1 g. samples of root from each of the five plants. When root systems weighed less than 1 g. the counts were converted to the 1 g. unit.

The open circles indicate the numbers of second-stage larvae, the blacked-in circles represent the total number of all larval stages found. The difference between these two values for each sampling date represents the number of larvae which have developed past the second stage, i.e. the stage at which the larvae invade the roots. No attempt was made to distinguish between third and fourth stage larvae since such distinctions are difficult under the dissecting microscope used for counting. Nearly all further development seen was of male eelworms, many of which appeared to reach maturity ; very few developing females were found.

The graph shows a steep initial rise in total larval numbers per gramme of root, reaching a maximum 20 days after the first appearance of shoots, followed by a steady decline. This fall coincides with the time at which the males developing from the first larvae to enter might be expected to mature. Many apparently mature males appeared in the samples at this time. The number of second stage larvae reached a maximum at 20 days also, after which the number per gramme of root diminished. During the period of most rapid invasion the proportion of second stage larvae was at its highest, though some larval invasion still occurred towards the end of the experiment.

A similar experiment using the susceptible variety Majestic showed that the same rapid initial invasion occurred, the number of larvae per gramme of

root reaching its maximum (2100) also at 20 days. The rate of decline in numbers was less rapid than for *S. andigena*, there being little change for almost 10 days after the peak was reached. A likely explanation of this difference is the presence of large numbers of maturing females which remained attached to the roots for a longer period than the males.

When a clone of *S. vernei* was examined in the same way the number of larvae found was much lower, the maximum being 600/g. of root, and very few of these had developed beyond the second stage. The low level of larval invasion and hatching factor production shown in the *S. vernei* clones tested suggests that they have a higher degree of resistance to potato-root eelworm than resistant *S. andigena* plants.

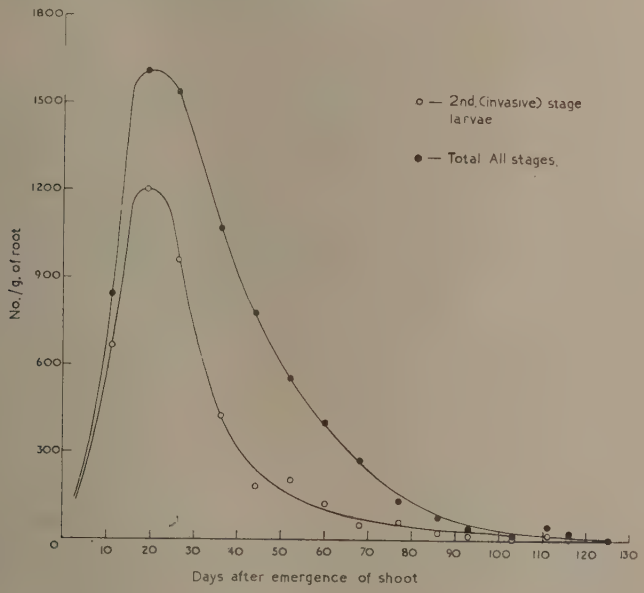


FIG. 3.—Larval invasion of resistant *S. andigena* plants.

Some caution is necessary in the interpretation of results in this type of experiment since the plant root system is increasing throughout, and although the number of larvae per gramme of root appears to reach a peak and then decline, the total numbers in the whole root system at the sampling dates may present a different pattern. Further investigations, using the whole root system rather than a representative sample of it, remain to be made.

Eelworm Population Changes Produced by Resistant Potatoes.

From the foregoing observations it might be expected that the eelworm-resistant forms of *S. andigena* would have a considerable effect on the eelworm population levels in infested soil. Field and pot experiments have been made to measure any changes which occur.

The first field trial was held on an eelworm infested site in Feltwell Fen, Norfolk, during 1955. Three resistant lines from *S. andigena* × *S. tuberosum* first crosses were used, together with the susceptible varieties Majestic and

Ulster Chieftain. A set of fallow plots was also included. The egg content per gramme of soil for each plot was estimated before planting and after lifting the crop. At the same time, a pot experiment was begun with the variety Majestic, one of the three resistant clones planted in the field trial (Z3/7), and a fallow treatment.

The population changes which occurred are shown in Fig. 4, in which the logarithms of the final populations have been plotted against those of the initial populations.

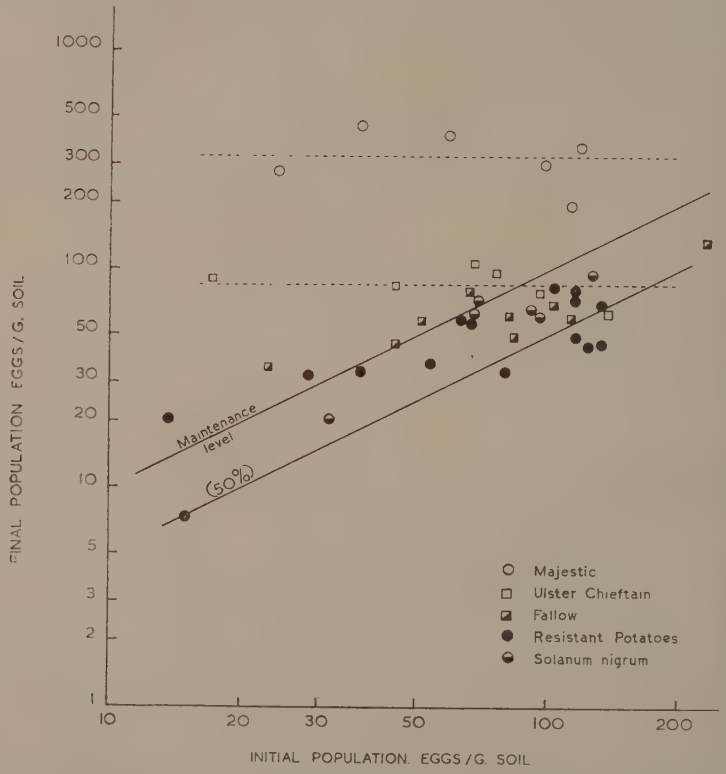


FIG. 4.—Relationship between initial and final eelworm population levels in the field trial 1955.

The maintenance level line has been drawn to indicate those points at which initial and final populations are the same. The lower parallel line joins those points at which the final population is 50 per cent of the initial one. Most of the plots in which resistant potatoes were grown had a final population well below the initial level. In the six plots planted with the most vigorously growing resistant potato (Z3/7) the mean reduction was to 48 per cent of the initial level. Both susceptible varieties caused the eelworm population to reach a " ceiling " level, i.e. the final population levels appeared to be independent of the initial ones (Jones, 1956). The " ceiling " levels are represented in Fig. 4 by the horizontal broken lines, the upper that for Majestic (4·4 × the

initial mean level for 6 plots), the lower for Ulster Chieftain which died off sooner.

Table II compares the results obtained from the field and pot experiments of 1955. The effects of both susceptible and resistant potatoes are more pronounced in the pot tests than in the field. This is largely because the roots explore the potted soil more thoroughly than the soil in field plots. Changes occurring near the roots of plants grown in field plots are minimized by the inclusion, in the sample, of soil from parts of the plot distant from the region of influence of the roots.

TABLE II.—Population changes occurring in pot and field experiments 1955.

Treatment	Pots $\left(\frac{\text{Final popn.}}{\text{Initial}} \times 100\right)$	Field $\left(\frac{\text{Final popn.}}{\text{Initial}} \times 100\right)$
Majestic . . .	8000	440
Fallow	49	77
Z3/7	20	48

Initial population levels. Pots—300 eggs/g. soil. Field—80 eggs/g. soil.

The pot tests were conducted under glass and all pots were well watered. These conditions served to accentuate any trends towards a reduction or increase in the population. Thus, although there is no question of thorough exploration of soil by root systems in the fallow pots, the reduction in population level was much more marked than in the field where conditions were unusually dry during the summer of 1955. The extremely dry conditions prevailing would be expected to reduce larval hatch and motility (Wallace, 1955).

The fall of 80 per cent in the pots containing Z3/7 plants is similar to that recorded by Peters (1953) and Fenwick & Reid (1953) using susceptible varieties. When soil samples were taken, just before the rise in egg content coincident with the maturation of the new generation females, these workers found that the egg content at its lowest level was between 20–30 per cent of the initial population. Their figures confirm the similarity between resistant *S. andigena* plants and susceptible potatoes in respect of hatching factor production and larval invasion.

The Effect of Eelworm Population Level on the Growth of Resistant Potatoes.

The yield figures of the 1955 field trial gave some indication that the growth of the resistant potatoes was adversely affected by high eelworm population levels. A second trial on the same plots in 1956 enabled a fuller investigation of this effect to be made. All plots were planted with clone Z3/7 and the population levels had a much wider range, from 447 eggs/g. soil after Majestic potatoes down to 7 eggs/g. soil after Z3/7. The results are shown in Figs. 5 and 6.

Fig. 5 shows the relationship between yield and the logarithm of the initial population (1956) for the 42 individual plots. The regression of yield on initial population has been calculated and the regression line is given.

The significance of the regression was tested by analysing the variance of the dependent variable (yield of plots) into its component factors. The regression coefficient was found to be significant at the 0·1 per cent level.

Few of the plots had similar eelworm population levels because of the original uneven distribution in the field and the further differences produced by the treatments in 1955. It was not possible, therefore, to have replicates of

a particular population level but the six plots in which Majestic potatoes had grown had distinctly higher populations than the remainder, constituting a clearly separate group. The remaining plots were arranged in groups of six in descending order of eelworm content. The estimated mean value of eggs/g. of soil has been plotted against the total and ware yield for each group of plots

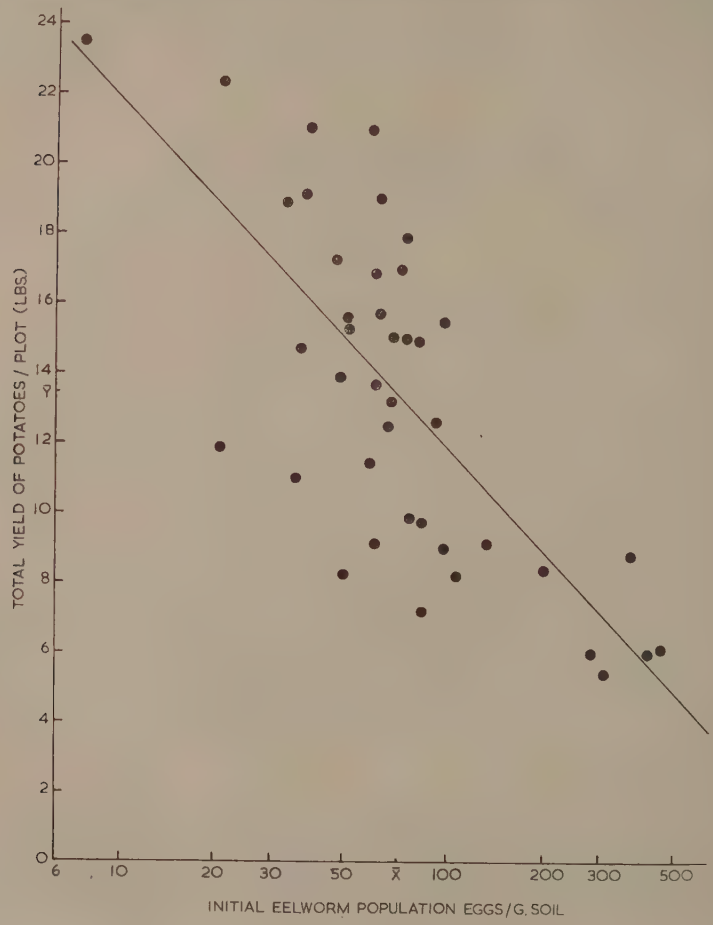


FIG. 5.—Relationship between initial eelworm population level and yield in the field trial of resistant potatoes 1956. Data for individual plots.

(Fig. 6). The six plots with the highest mean population level (332 eggs/g.) yielded 40 lb. total weight of tubers, the six plots with the lowest population levels (25 eggs/g.) produced a total of 102 lb.

This check to the growth of resistant potatoes was confirmed in pot tests and other small scale field tests made during 1956. The results of all these tests indicate that "eelworm-resistant" potatoes are adversely affected by larval invasion. The giant cells which disrupt the phloem have been found associated with developing male larvae in resistant plants. Whether such

plants are injured in other ways, e.g. by production of toxic substances by the giant cells or the developing larvae is not known. The injury sustained by resistant plants does however appear to be relatively less than that suffered by susceptible plants. This may be due to the greater withdrawal of nutrients from susceptible plants by the developing females which attain a greater size and remain feeding on the roots for a longer time than do the males.

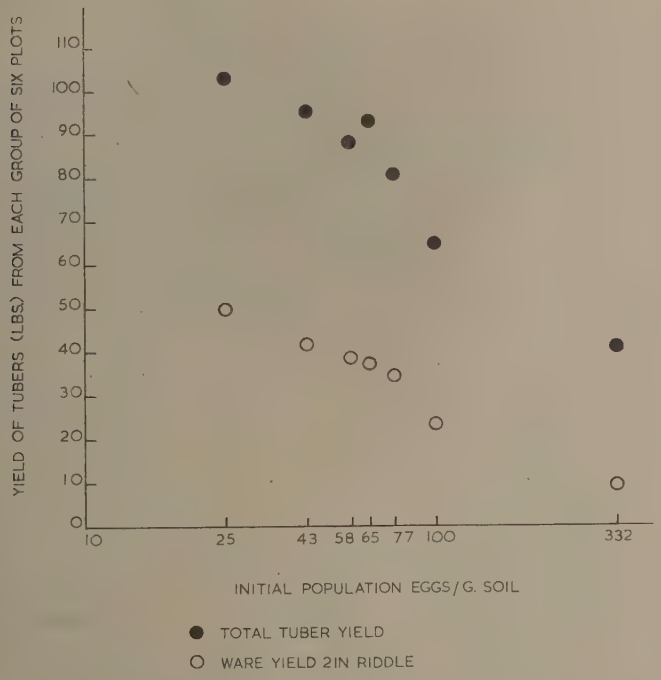


Fig. 6.—Relationship between initial eelworm population level and yield in the field trial of resistant potatoes 1956. Data for each group of six plots.

Eelworm Population Changes Over the Two-year Trial Period.

It is now possible to compare the effects of two years of various sequences of plant and fallow cultivations on the population levels existing at the beginning of 1955. It must be emphasized however that these results apply to only one soil type, the black fen, and that both growing seasons were far from the 30-year average in respect of rainfall, 1955 being a very dry summer, 1956 a very wet one.

The changes which occurred are shown in histogram form in Fig. 7. Comparisons have been made between three series, each of six plots: series A, in which Majestic potatoes were grown in 1955, series B, which was left fallow that year, and series C, in which the most effective resistant potato clone Z3/7 was planted. The changes which took place during this first year were as follows. Majestic potatoes caused an average increase of 4·4 times the initial population, the fallow plot population fell to 77 per cent of the initial population, and the resistant potatoes caused a fall to 48 per cent.

In 1956, resistant potatoes were grown on all plots, and reductions occurred in all three series. The percentage figures given with the mean values for eggs/g. soil in the lower set of histograms indicate the relationship between the initial population levels for 1955 and the final levels at the end of 1956.

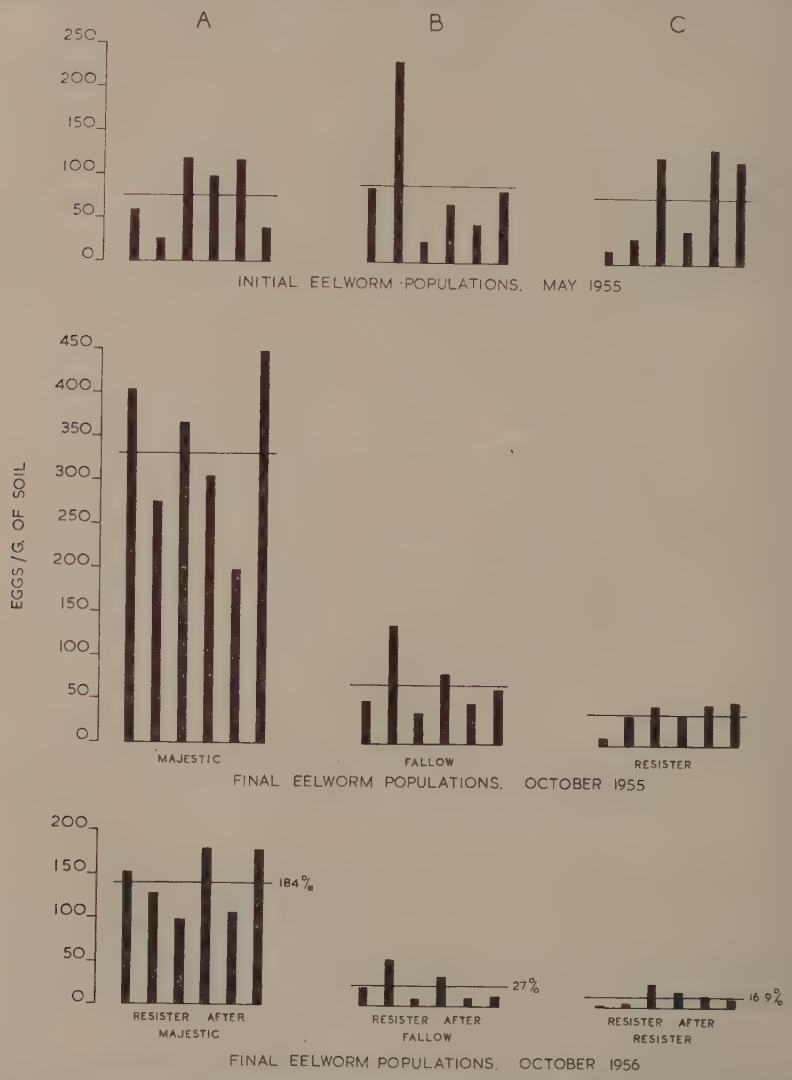


FIG. 7.—Comparison of changes in eelworm population levels during the two field trials.

DISCUSSION.

The breeding programmes for the production of commercially acceptable eelworm-resistant potatoes are now well advanced. Both in Britain and in Holland, plants combining the features of resistance described in this paper

with qualities approaching those of existing commercial varieties are being grown on an increasing scale. The field and pot experiments at Cambridge have shown, as suggested by observations on hatching factor production and larval invasion, that such resistant potatoes can considerably reduce the eelworm population levels in certain infested soils.

However, a complication has arisen with the discovery of a new strain* of *Heterodera rostochiensis*, first observed in Scotland (Dunnett, 1957), and now known to occur widely in many parts of Britain (Jones, 1957). This strain is able to reproduce freely on plants hitherto thought to be resistant. Jones has found some 2000 cysts on plants which, after repeated testing at Cambridge, developed a maximum of four or five cysts only. It is fortunate that this new strain was not present in the soil used for the first screening tests in Newcastle, Holland, Cambridge and Edinburgh, otherwise the existence of some *S. andigena* plants which are resistant to many eelworm populations might not have been detected.

It was thought that the few cysts which occur from time to time at Cambridge on resistant plant roots may have developed from larvae capable of breaking down the resistance, but attempts to re-infect the resistant plants using these cysts have shown that their contents stand no better chance of maturing into females than larvae from cysts taken at random from the populations used. It may be that the larvae in such cysts are not necessarily all resistance-breaking individuals. The numbers of resistance-breaking larvae might depend on the genotype of the parents and whether the factors conferring the ability to break resistance are dominant or recessive. The genetics of resistance-breaking strains has recently been discussed in more detail by Jones in a paper given at the 1957 Plant Protection Congress in Hamburg. An alternative explanation of the occurrence of these few cysts is that local breakdowns in the plant's resistance mechanism occur.

Although the resistant plants developed at Cambridge have continued to reduce the eelworm populations in the Feltwell soil, it is possible that further planting of them might increase the population of any resistance-breaking eelworm strains present in amounts not detectable at present. Commercial potato varieties must be hosts of the new strain since it occurs widely in fields where resistant potatoes have never grown, and it has been found to multiply rapidly in pot tests using susceptible varieties. Only continued planting of hitherto resistant clones will detect increases in the new strain.

The most that can be said at the present time is that the existing resistant potatoes should be of value in reducing eelworm populations of the non-aggressive strains. This has occurred on the Feltwell site where a reduction to 16·9 per cent of the initial population has occurred after two years resistant potato-growing. Although reductions of yield occurred when the eelworm populations were high there was no crop failure and the plants reduced the eelworm population effectively. This reduction lessens the effect of eelworm injury in the succeeding year.

If the new eelworm strain does not increase rapidly, or at all, in such areas then eelworm-resistant potatoes derived from *S. andigena* will still be of value when grown in rotation with other non-host crops.

The low production of the hatching factor, and the greatly reduced larval invasion with little subsequent development, have previously been suggested as indicating a higher degree of resistance in *S. vernei*. Tests made by Jones and Dunnett, using the new eelworm strain against several clones of *S. vernei* have so far shown its resistance to be maintained. Attempts at breeding from

* It is not yet known whether one or more distinct strains occur in the numerous resistance-breaking populations so far detected.

S. vernei in Germany (Goffart & Ross, 1954) have met with difficulties since the expression of its resistant factor appears to weaken during back-crossing. Apart from this it is very wild in character and under long day conditions produces many long stolons with very few small tubers. However, if these problems can be overcome it may prove to a be valuable source of resistant material; Ross (unpublished work) considers that the *S. vernei* material now being used in Germany might constitute such a source.

Acknowledgments.

The work described in this paper forms part of an investigation financed by the Agricultural Research Council. I would like to thank Dr. H. W. Howard of the Plant Breeding Institute, Trumpington, for supplying the eelworm-resistant potatoes used, and Mr. F. G. W. Jones of the Nematology Department, Rothamsted for his continued interest and advice. Thanks are also due to Mr. A. S. Rickwood of Chatteris for his kindness in making the field trial site available.

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On a Disease Complex of Strawberries Involving a Nematode and a Bacterium. By Dr. R. S. Pitcher and Dr. J. E. Crosse.

The symptomatology of the disease of strawberries attributed to nematodes of the genus *Aphelenchoides* has been complex and confused. This paper describes experimental investigations of the condition known as Cauliflower Disease. Two agents, a nematode, *Aphelenchoides ritzema-bosi* (Schwartz) Steiner and a bacterium, *Corynebacterium fascians* (Tilford) Dowson were inoculated separately and in combination. Initial experiments with vegetatively propagated plants in open pots proved that both organisms are essential, but the relative role of each was obscured by the ubiquitous distribution of "wild" strains of the bacterium. This problem was overcome by the use of seedling plants and pure culture techniques. It was then possible to analyse the cauliflower complex more precisely and to assess the role of each agent in this and other related diseases of strawberry.

Part of the work described in this paper has been published. (Crosse, J. E. and Pitcher, R. S. (1952). Studies in the relationship of eelworms and bacteria to certain plant diseases. I. The etiology of Strawberry Cauliflower Disease. *Ann. appl. Biol.*, **39**, 475–484) and the remainder is to be published shortly, probably in *Nematologica*.

SYMPOSIUM ON WEED KILLERS

Weed Control in Crops. By Professor R. L. Wain, Wye College, University of London.

To be phytotoxic, a chemical must be able to enter the plant and move without breakdown through its tissues to the "sites of action" from which are initiated the complex series of processes leading to the death of the plant.

These properties of a compound depend on its chemical structure and, to a certain extent, on how it is made up for use as a herbicide. Much research is being undertaken at the present time on herbicidal action in relation to physical properties and to chemical structure, and as a result the search for new and improved materials is becoming more logical and less empirical.

From the agricultural viewpoint by far the most important herbicides are those which can be used to destroy weeds growing with useful crops. The "selective" action of such chemicals can arise in a number of ways.

Sulphuric acid, as is well known, can be used to destroy broad-leaved weeds growing with cereals. The selectivity here depends mainly on differences in morphology and habit of growth between crop and weed. Because of their tall erect growth and the waxy nature of their leaves, cereal plants do not become well wetted by the spray as do weeds with flat horizontal leaves like charlock. In this way, by a differential wetting effect, cereal plants largely escape the toxic effects of the chemical whereas many weed plants are destroyed. Sulphuric acid can also be used as a "pre-emergence" treatment for example with a crop such as the onion. If the spray is applied just before the onion seedlings appear through the ground, all the small weeds can be eradicated

without damaging the crop. In this case, the selectivity depends on the physical protection of the seedlings provided by the thin layer of soil above them. Other pre-emergence weedkillers, e.g. trichloroacetic acid, exert a toxic action in the soil upon germinating weed seeds and not on those of the crop. Most of the compounds used in this way have been arrived at by empirical testing methods and the reason for their selective action is usually obscure.

The most important group of selective herbicides are phenoxy acids such as 2-methyl-4-chlorophenoxyacetic acid (MCPA) and 2,4-dichlorophenoxyacetic acid (2,4-D). Such chemicals have arisen from research on plant growth hormones and, indeed, the herbicidal properties of these compounds depend on the drastic effects they produce on the growth of certain plants when applied at rates sometimes as low as 4 oz. per acre.

These "hormone" weedkillers, which are non-poisonous to man and animals, are absorbed by leaves, stems and roots and are translocated through the tissues. Cereals and grasses, however, are more resistant to their action than many weeds and this makes it possible to use MCPA and 2,4-D as selective weedkillers in these crops. Whilst millions of acres of cereal crops are sprayed annually with MCPA or 2,4-D, it is not safe to spray with these chemicals until the crop plants have tillered owing to the danger of inducing malformations in the heads at a later stage in growth. Again, these weedkillers are damaging to clover and lucerne, both of which are often sown with cereal crops.

Such difficulties have been largely overcome by the discovery by the writer of a new group of selective weedkillers with a unique mode of action. The specific activity of these new chemicals, of which 2-methyl-4-chlorophenoxybutyric acid (MCPB) and 2,4-dichlorophenoxybutyric acid (2,4-DB) are examples, arose from fundamental investigations on the breakdown of substituted fatty acids within plant tissues. This work established that β-oxidation, a process well known to occur in the animal body, was also a means by which fatty acids became degraded in plants. Furthermore, it was found that the β-oxidase enzyme systems present in different plants possessed very specific activity. Thus the compound MCPB, harmless *per se*, was degraded readily by β-oxidation to the highly active growth substance MCPA within the tissues of many plants including a number of important weeds. These plants thereby destroyed themselves. Certain crop plants on the other hand such as clover, did not possess this same capacity to convert MCPB to MCPA and therefore suffered little damage.

Similar results were obtained with other compounds which were capable of being degraded to an active weedkiller by β-oxidation. These findings have led to important developments* and at the present time MCPB and 2,4-DB are being used in a number of countries for specific weed control operations where hitherto chemical control was not possible. This unique type of activity where the chemical breaks down to an active herbicide within the tissues of one plant and not in another, represents a new approach to selective weed control.

* See Wain, R. L., *Ann. Appl. Biol.*, **42**, 151 (1955).

Wild Oats. By Dr. J. Stubbs.

Few weeds of arable land are so difficult to eradicate as wild oats (*Avena atua* L. and *A. ludoviciana* Durieu).

The biological features of these two weed species were described in relation to their control by cultural methods and by chemical treatments.

THE USE OF SELECTIVE WEEDKILLERS IN THE CONTROL OF VEGETATION ON ROADSIDE VERGES. By Miss OLIVE BALME.

The roadside verge habitats are of considerable ecological interest but very little work has been carried out in this field. The Nature Conservancy were therefore concerned about the possible threat to the natural flora and fauna arising from the use of selective weedkillers to replace cuttings of verge vegetation. Experiments were carried out to show the effects of two preparations of 2,4-D on a number of sites sprayed for two or four successive years.

THE POTENTIAL VALUE OF HERBICIDES IN NATURE RESERVES. By J. D. FRYER, A.R.C. Unit of Experimental Agronomy, University of Oxford.

Much of our work at Oxford is concerned with the selective control of weeds in agricultural crops but we try to maintain an interest in the possible application of the many highly phytotoxic and selective compounds that are now available wherever the control of unwanted vegetation is a problem. We have found that the practical study of herbicides can logically be divided into two phases. First, there is the preliminary testing of the toxicity of a new herbicide to individual crop and weed plants, little reference being made to practical problems of weed control except as a guide for choosing the species under test. This phase may be regarded primarily as an occupation for the specialist who has a knowledge of the action of herbicides and is in a position to develop special techniques and equipment for his study of toxicity. The second phase is to make use of this knowledge to find out the value of a promising herbicide for the solution of specific problems, where it is desired that unwanted plants are to be controlled. This is best carried out by the specialist on weedkillers in conjunction with those who are experts in the problem itself.

Working in this way we have co-operated with many organizations and individuals who have been faced with specific problems both in this country and in the Colonies. One instance was the testing of herbicides for the control of vegetation on roadsides in conjunction with the Nature Conservancy and we have heard some of the results from Miss Balme this afternoon. All the problems have had one thing in common : man's desire to interfere with nature by trying to help some plants to grow at the expense of others.

Those concerned with the conservation of Nature Reserves are sometimes faced with similar problems of how to control some plants without affecting others. Changes in environmental conditions can result in an upsetting of the many factors responsible for the desired type of plant community and, if a community is not to change and lose much of its value as a Nature Reserve for scientific study or as a living museum of rare plants, treatments may have to be introduced which will restore and maintain the desired flora. For instance at one fenland nature reserve which I know well—Woodwalton—one of the main costs of maintenance is the cutting by hand of the sallow bushes that constantly invade parts of the fen. Chalk downland also presents a problem where the cessation of grazing by rabbits and sheep tends to lead to domination by coarse grasses such as species of *Brachypodium*, or by hawthorn or brambles, to the detriment of many interesting plants. At present the control of such unwanted plants is generally thought of in terms of traditional methods such as cutting and grazing and where these are not possible often nothing is done to prevent the establishment and spread of the invading plants. Herbicides

have not, as far as I know, been extensively tested as alternative methods of control in this country but in the United States, according to figures published by the Department of the Interior, nearly 14,000 acres of the national wild-life refuges were sprayed with herbicides in 1955 at an average cost of 1·64 dollars per acre.*

My object in giving this paper is to review in very general terms some of the less well-known capabilities of the present-day herbicides that may have some application in Nature Reserves in this country. Perhaps I should say that I speak only as someone who knows about the chemical methods and not as an expert on the problems of nature conservation.

I propose to divide the subject into three headings : the control of woody plants, the control of herbaceous plants, and the control of aquatic plants.

Woody plants can be prevented from invading an area by suitable management which is generally based on cultivation, grazing, mowing or burning. Sometimes, for instance with gorse or brambles, these treatments can be ineffective or possibly the nature of the area does not permit the necessary management to be carried out at reasonable cost. The spray application of a herbicide such as MCPA, 2,4-D or 2,4,5-T may then prove useful in selectively killing the young plants in a grass sward before they become established. Overall applications to a large area would, no doubt, be unacceptable on conserved areas on account of the effect these chemicals are likely to have on some desirable broad-leaved species but it may on occasion prove practicable to treat local areas of the invading plants before they become too widespread.

With an area of established scrub, the conventional methods of clearance are based on cutting or digging by hand or mechanical means or by girdling the stem of larger trees. Frequently such methods offer only temporary control because of suckering or coppicing from the roots or stumps left in the soil. Nothing short of digging up the plants, an expensive business, gives long-lasting results and subsequent maintenance costs may be high. For problems such as this, herbicides have already proved their value in forestry work and in land-reclamation for agriculture in many parts of the world, the main applications being the killing of unwanted trees in indigenous forests, the control of scrub and regenerating stumps in woodland that has been cleared and replanted and the reclamation of grazing land from unproductive scrub. The main chemical used for the control of woody plants is the plant growth-regulator 2,4,5-T. It can be applied in a variety of ways, probably the most useful being what is called the basal-bark technique, in which a solution of 2,4,5-T in a cheap oil such as diesel fuel, vaporizing oil or used engine oil is painted or sprayed onto the basal foot or two of the stems. The treatment can be carried out at any time of the year and will kill a wide range of tree and shrub species including Sycamore, Birch, Hazel, Poplar and Willow. One of the advantages is that all the chemical applied goes on to the woody plants and none on to the herbaceous vegetation. A truly selective control is therefore obtained.

Where the scrub is too thick to permit individual treatment of the standing plants, there are two alternative methods of applying 2,4,5-T. The scrub can be cut over and the stumps sprayed shortly afterwards with a solution of 2,4,5-T in oil, again using a directed application, or the chemical can be applied in an oil/water emulsion as an overall spray to the foliage during summer. The latter method requires power-operated spraying equipment and is not effective on such a wide range of species as the basal bark and stump treatments, which can be applied by an ordinary knapsack sprayer or even a paint-brush. It is also often undesirable because of the unsightly death of the foliage and the

* Ref.: *Summary of Weed Control on National Wildlife Refuges*—1955. Compiled by W. B. Stiles, U.S. Dept. of the Interior, Fish and Wildlife Service, Washington 25, D.C., 23 March 1956.

effects on broad-leaved herbaceous species. One application for which summer spraying is particularly valuable is the control of established brambles.

The most important feature of scrub control by chemicals is that a complete kill of all plants should not be expected after a single application. Neither the chemicals nor the application methods are good enough to permit this at reasonable cost and many people are disappointed because a year after treatment some of the treated plants are producing new growth from the roots or because new seedlings are evident. The working principle should be that chemical treatment must be followed either by suitable management which will discourage regrowth from affected but still living plants and will also prevent the establishment of seedlings, or by occasional repeat sprayings to deal with survivors or new invaders. Obviously, if the environment is not changed, further invasion is likely to occur whatever control method is used. However, individual chemical treatment of surviving woody plants or invading seedlings can often easily and cheaply be made as required in the years following the initial herbicide treatment and this may be a much more practicable maintenance treatment, where a limited labour force is available, than repeated cutting of, for instance, a dense stand of scrub. Some species such as hawthorn and rhododendron are difficult to kill with 2,4,5-T and the best chemical treatment for these is probably the application of ammonium sulphamate to stumps after cutting.

Most of the work on woody plant control has been done with 2,4,5-T, ammonium sulphamate, 2,4-D and sodium arsenite, which can all be very effective but there are several other compounds which might prove more efficient for particular species and problems. These include the substituted ureas, the subsituted benzoic acids and various phenoxy-acetic, -butyric and -propionic acids. Unfortunately this branch of the study of herbicides tends to be somewhat neglected in this country ; much more work is required before the true usefulness of the techniques I have mentioned can be assessed for the many different herbicides that are potentially useful.

The control of herbaceous plants in nature reserves may, I imagine, be of interest in at least three ways. Firstly, stands of undesirable or uninteresting species such as nettles may be present, secondly there may occur species such as ragwort, thistles and docks, which must by law be cut down or destroyed to prevent seeding and, thirdly, ecologists may wish to study the colonising powers of various plant species to assist them in planning a programme of management for the maintenance or alteration of existing plant communities. For all these problems, the existing herbicides may have a useful part to play. Most broad-leaved plants can be killed by one or other of the several synthetic growth-regulator herbicides and each compound has different selective properties, affecting some species and not others, which may suit it for a particular purpose.

The new herbicide dalapon will kill many grass species when sprayed on to the foliage and its effectiveness and comparatively low cost make it extremely interesting not only from the point of view of grass control on the banks of dykes and ditches or in firebreaks, but also as an experimental tool for the destruction of the grass components of a plant community. Like all herbicides it has selective properties when used at low dosages but relatively little is known about its effect on wild plants in this country.

Lastly, there are the chemicals that can be used for aquatic weed control.* There is at the present time in this country, a great interest on the part of those concerned with the maintenance of waterways, drainage canals, dykes and reservoirs in the chemical control of the aquatic weeds that are the cause of heavy maintenance expenditure on mechanical means of control. Areas of

* Recently summarized by Aylwin P. Chancellor in *Ministry of Agriculture, Fisheries and Food Bulletin*, " The Control of Aquatic Plants and Algae ".

fenland, marsh and swamp that are conserved as nature reserves present similar problems. These can be divided from the point of view of chemical control into those where floating and submerged aquatic plants including algae are troublesome, and those where plants, such as reeds, bulrushes and sedges, which grow in shallow water, need to be controlled. Several herbicides are proving effective against the latter and preliminary trials have shown that dalapon and the substituted ureas are particularly promising. The Nature Conservancy are conducting trials with these and other chemicals for the control of *Spartina* on tidal mudflats. For the submerged species, sodium arsenite at 2–6 p.p.m. is still a standard treatment and contrary to popular belief the chemical is not toxic to fish at this concentration. For the control of algae copper sulphate at a concentration of 0·5–1·0 p.p.m. is generally recommended and can easily be applied either to flowing or static water. A new chemical, dehydroabiethylamine acetate, is also showing promise in the United States as an algicide.

There is no time to describe the details of these treatments or the experimental work that has been carried out, but I hope I have given sufficient information to convince you that these new herbicides are worthy of consideration whenever problems of vegetation control are encountered. It is unlikely that sufficient information is available on which to form a sound opinion of their value in terms of effectiveness and economy for any particular problem at the present time, because of the small amount of research that has been carried out in this country. For my part, I can only offer to give such assistance, as I or my colleagues at Oxford can to anyone who would care to try them out themselves for their own particular problem.

Lastly I might add that most of the weedkillers I have mentioned are relatively non-toxic to human beings and animals.

SYMPOSIUM ON CYTO-TAXONOMY.*

Introduction. By W. B. Turrill, O.B.E., D.Sc., F.L.S., V.M.H.

Cyto-taxonomy presumably means the application of cytological data to taxonomy. I have some knowledge of what taxonomy is and some ideas as to what it should be. For the moment, may we say that taxonomy is the determination of the different kinds of plants and animals, their grouping into various grades, and consideration of the principles by which this grouping is made. Cytology is, or should be, the study of the cells of animals and plants. Taxonomy has a longer history than cytology and is a less specialized subject. One usually finds that taxonomists have wider outlooks and are more generally enlightened than cytologists, excepting, of course, those who are to speak to-day. It is worth emphasizing that cytology is the study of animal and plant *cells* because all too often it is taken nowadays to mean only the study of chromosomes or at most of the nucleus and its make up. In other words, cytology is wrongly made synonymous with karyology—the whole being reduced to a part. This is not to dispute the unique importance of nuclei and of chromosomes but to plead that the cytoplasm, plastids, and all material in cells should receive due attention and that their relevance to taxonomy should be considered.

A word of warning, especially to taxonomists, is also advisable in connection with chromosomes themselves. So often chromosome number is assumed to be the all important, if not the only, chromosome character of interest to taxonomists, but size, shape, and behaviour of chromosomes may throw more light on a taxonomic problem than their number alone. Taxonomists should

* See *Nature, Lond.*, **179** (1957), 1274, for further account.

not be content merely to look up a species in the Chromosome Atlas and crib its chromosome number. They should consult the reference or references to original works and give proper consideration to any other chromosome characters there described.

There are apparently still some taxonomists who argue that a general taxonomy is impossible, either on theoretical or on practical grounds. They would limit taxonomy to what can be seen of gross morphology with the naked eye or a simple hand-lens. The best reply to such an argument is to refer to the increasing amount of synthetic taxonomy that is being produced and the greatly improved classification that results when all determinable characters derived from morphology, anatomy, cytology, genetics, phytogeography, ecology, and even pure physiology are used. One has, however, to realize that it has been generally much easier to obtain the facts of gross morphology than of the other branches of botany just mentioned.

We have relatively full data for gross structure of a much greater number of species than we have for their cytology. It is risky for cytologists who have examined the chromosomes of one or a few samples of a few species of a flora or of a family to attempt to correct too dogmatically the findings of taxonomists even if these have been based mainly on gross morphology. Few cytologists, it would seem from their publications, realize the vast wealth of many floras, especially of the tropics and subtropics. Moreover, a large number of cytological records are based on examination of single plants or of plants from one locality, and that very often a botanic garden. A taxonomist suspects that there may often be cytological variation corresponding with the variation in other characters he finds so characteristic of species. It may also be noted that the value to the systematist of much cytological research is greatly enhanced when it is combined with genetical experiments.

There is one other matter that taxonomists regard as having great importance. With all its faults and difficulties, the orthodox herbarium method of taxonomy does mean that the basic material described and classified is permanently preserved. Determinations can by its use be checked, mistakes rectified, and improvements in classification based on increased knowledge made. Unless cytologists preserve adequate specimens of the actual plants they have examined cytologically it is often not possible to confirm or correct with certainty the determinations they have made or accepted. When cytological findings do not agree with previously accepted taxonomy, it may be that the old taxonomy is wrong, it may be that the new cytology is wrong, or it may be that the cytological findings have been recorded under a wrong plant name. One has to eliminate two out of three possibilities to find and correct the error in the third. A great deal of time and trouble may be saved if properly prepared voucher specimens be preserved.

May one who is whole-heartedly in favour of synthetic taxonomy say that, in common with many of his colleagues, he welcomes any and every contribution that cytologists can make towards elucidating the problems of taxonomy in the widest sense. The number of botanists who regard cytologists as queer perverse ultra-modernists who "peer down a microscope and count their own eye-lashes" is dwindling. On the other hand, the taxonomist may be somewhat irritated by the recent declaration of a karyologist that the "fictions, errors and half-truths" of taxonomy "can be quickly remedied by a study of the chromosomes" (Darlington, *Chromosome Botany*, p. 32 : 1956). It is nonsense to pretend that scoring the chromosomes tells one everything one needs to know about a plant. Plant cytology is but one of the branches of botany from which taxonomists desire to have an increasing number of facts relevant to the construction of a sound general classification. There is, however, nothing to prevent cytologists constructing their own classifications—

one or more per cytologist—based solely on cytology or some part of it. The results of such attempts would be most interesting. Personally, I think that the right way to advance in our knowledge of plant life has been indicated by Babcock and his associates in the genus *Crepis* and by Goodspeed and his associates in *Nicotiana*. Those who follow me to-day will illustrate some of the contributions made on this side of the Atlantic. Exaggerated claims or extreme criticisms made by taxonomists or by cytologists are to be deplored. What is needed is co-operation based on an understanding of each others' aims and methods and expressed in attempts to synthesize results.

Problems in Mammalian Cytotaxonomy.

By J. L. Hamerton, B.Sc., A.R.C.S., F.L.S., British Museum (Natural History).

(With 9 Text-figures.)

Introduction.

In the better known groups of plants and animals a study of the chromosomes has for many years served as a valuable adjunct to taxonomic research (White, 1954, 1957; Darlington, 1956).

In mammals, cytotaxonomic research has in the past been considerably handicapped by inferior and more complicated technical methods, with the result that in the latest check list (Tobias, 1956), less than 3 per cent of the known mammalian species are listed as having been cytologically examined. When this is compared with plants where the chromosomes of some 15–20,000 species are recorded (Darlington & Wylie, 1955), it becomes clear why chromosomes have, up to the present, played so little part in mammalian taxonomic research.

In the present paper, it is intended to review the available data in an endeavour to make some assessment of the value which cytological research in mammals is likely to have in the solving of current taxonomic and evolutionary problems.

Technical Methods.

In the past ten years, technical methods used in the study of mammalian chromosomes have been revolutionized, so that it is now possible to make a detailed analysis of the chromosomes of the majority of mammalian species with no more difficulty than is generally experienced in the handling of most plant or insect chromosomes.

Improvements in technical methods may be divided into four distinct and separable stages, which are summarised as follows :—

(i) The use of hypotonic solutions of various kinds for the purpose of swelling the cells in order to obtain improved chromosome separation (Makino & Nishimura, 1952; Hughes, 1952).

(ii) The successful use of simple fixatives, such as acetic alcohol, or acetic acid, for fixation of mammalian chromosomes (Sachs, 1952, 1953).

(iii) The use of colchicine, administered by injection, to accumulate mitoses and clarify chromosome morphology (Ford & Hamerton, 1956).

(iv) The development of techniques for the handling of somatic tissues as cell suspensions wherever possible (Ford & Hamerton, 1956).

Finally, improvements in tissue culture technique are now making possible detailed study of the somatic chromosomes of those species such as man and the larger primates, where colchicine injection into the living animal is clearly impracticable. In this way tissues may be removed from the animal by means

of biopsy, cultured for a short while, treated with colchicine and examined, thus obtaining the same clarity of observation as can be seen in preparations from small mammals which can be injected and handled in the laboratory.

Principles of Chromosomal Change.

(i) *Constancy of chromosome number.*—The concept that the diploid chromosome number of a morphological species is invariably the same, no matter from what portion of the range of that species the individual examined has been derived, is now known to be incorrect. It has received artificial support from the cytological practice of examining a very few specimens from each species, in order to make chromosome determinations. If, however, the Neo-Darwinian concept of evolution is accepted as one in which natural selection acts upon genetic variability, giving rise to discontinuities between populations, which in turn through isolation may eventually lead to the formation of a new species, it is only to be expected that in groups such as mammals, where a wide variation in chromosome number and morphology occurs between closely related morphological species, that a similar but narrower variation will occur within populations of the same morphological species. Such intra-specific variation is, of course, well known in invertebrate groups (White, 1956; Smith, 1956 *a* and *b*; Wahrman, 1954; Staiger, 1954); recently similar cases have been reported in mammals (Wahrman & Zahavi, 1955; Sharman, 1956; Ford, Hamerton & Sharman, 1957), and will be discussed at some length later. Darlington (1937), has pointed out that every gradation is found between structural, numerical and genotypic differences in the chromosomes on the one hand, and systematic differences on the other. The idea that chromosome change in itself must have some immediate genetic effect is an oversimplification. As Darlington (1937) has pointed out, its action may simply be to condition a genetic isolation of populations and hence a reduction in gene flow, which may then lead to eventual specific differentiation.

(ii) *Aneuploidy* (*Polysomy*).—Loss and addition of individual chromosomes is likely to have played little part in the evolution of mammalian caryotypes. Reports of somatic aneuploidy (Therman & Timonen, 1951, 1956; Manna, 1955) and others, should be treated with reserve, as it seems likely that some, at least, may have arisen due to faulty technique (Hsu & Pomerat, 1953; Beatty, 1954; Sachs, 1954; Ford & Hamerton, unpbl.).

(iii) *Polyploidy.*—A recent review by Beatty, (1957), deals very fully with the question of polyploidy in mammalian development. In particular, this work deals with the experimental approach to the study of polyploidy in mammals. Polyploids are of two types, allopolyploids and autopolyploids. The former are produced by a doubling or non-reduction of chromosome number in a hybrid, and the latter by the simple doubling of chromosomes without the intervention of hybridization (Darlington, 1937). In autopolyploids, a high degree of multivalent association will occur at meiosis, with probable resultant breakdown of pairing and segregation, and such forms are unlikely to survive in bisexually reproducing species, and can therefore largely be ignored in the present discussion. Allopolyploids, on the other hand, by virtue of their formation from the doubling of the chromosome number of a hybrid between two diploids, will enable normal bivalent association and segregation to occur at meiosis, and may therefore act to restore fertility of an otherwise infertile diploid hybrid. Muller (1925), has suggested that polyploidy is unlikely in bisexually reproducing species due to the disturbance in the sex-determining mechanism. Such disturbance could be of two types :—

(*a*) Failure of proper pairing and segregation of the X and Y chromosomes.

(*b*) Unsuitable balance between the sex chromosomes and the three or four sets of autosomes.

The first point is unlikely to be any great obstacle to the formation of allo-polyploids, where the sex chromosome constitution will be XX′–YY′, so that pairing will be between XY and X′Y′, with the resultant normal segregation (fig. 1). The question of sex chromosome to autosome balance is more difficult to answer. Darlington (1953), has suggested that the balance mechanism of sex determination which is found in *Drosophila* is unlikely to be so highly developed in mammals, and considers that something approaching a trigger mechanism may be more likely. If this is the correct view, then it would seem to be less of an obstacle to polyploidy than has been thought. Furthermore, sex determination in allopolyploids (fig. 1), is likely to be little obstacle to normal development, the autosomal sex chromosome ratio in the zygotes, XXXX ♀–XXYY ♂ being normal. The balance is, however, changed in the zygote XXXY, which may therefore be less viable or result in intersexes.

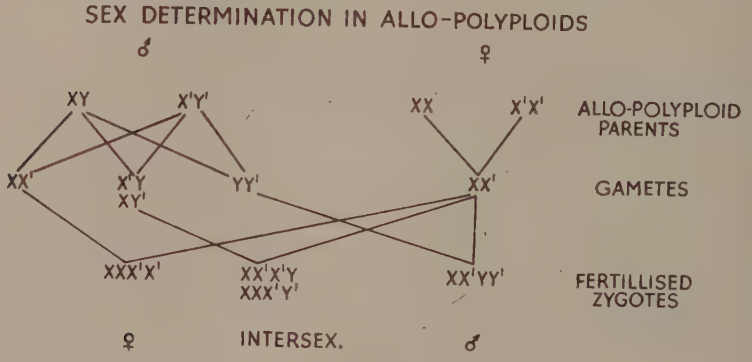


Fig. 1.—Sex determination in allopolyploids.

(iv) *Structural change.*—Clearly the most important type of chromosomal rearrangements are those which lead to viable gametes containing an altered chromosome complement. Only under these conditions will the altered caryotype stand any chance of being disseminated throughout the population, leading eventually to a polymorphic state on which selection is able to act. For the purposes of this discussion, types of structural changes will be divided into two :—

(*a*) Structural changes which lead to an alteration in the position of the centromere.

(*b*) Structural changes not involving the position of the centromere.

(*a*) Structural changes involving the centromere. The principal types are shown (fig. 2), and it will be observed that the first four types involve alteration in the chromosome number without any concurrent alteration in the number of chromosome arms, whilst the remainder result in an alteration of chromosome morphology without any alteration in chromosome number. Robertson (1916) recognized this first type of change, and used it to account for the relationship between acrocentric and metacentric chromosomes in certain groups of grasshoppers, and it has therefore since that time been described as Robertsonian variation. Matthey (1945), has shown that variation of this type, commonly and incorrectly known as " Centric Fusion ", has accounted for a large part of the visible differences between the chromosome sets of certain Lacertilia. In an attempt to apply this principle to other groups, Matthey (1945), coined a new term, " Nombre fondamental ", (F.N.) or Fundamental

Number, to describe the total number of chromosome arms in a caryotype. However, in mammals, as Matthey himself (1956*a*), has pointed out, there is no clear cut distinction between metacentric and acrocentric chromosomes, as every degree of intermediate form occurs. We find then, at the present time, that the decision whether a chromosome deserves an F.N. of one or two, whilst

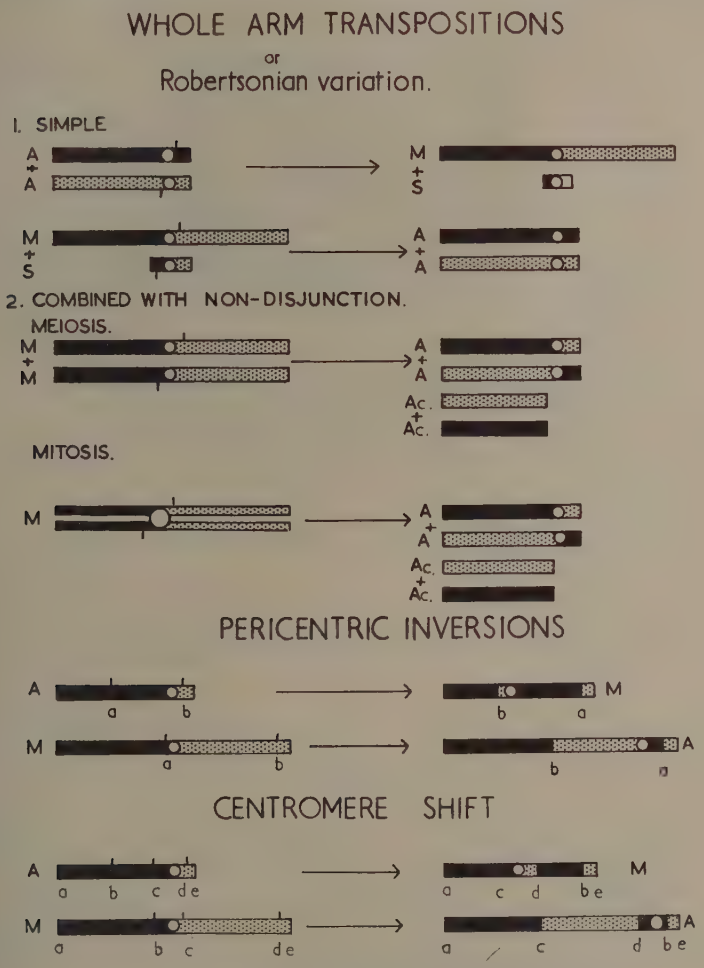


Fig. 2.—Chromosome rearrangements involving an alteration in the position of the centromere.

being clear enough in extreme cases, is largely subjective and depends on the preference of individual authors in the more intermediate type of chromosome. It is, therefore, important that if the F.N. is to be of any value as a measure of Robertsonian variation, it should be more clearly defined, so that comparison is facilitated. Furthermore, although Robertsonian variation has undoubtedly played a large part in chromosomal evolution in animals, it is neither the only,

nor necessarily the most important factor, and it is therefore suggested that the term "Fundamental Number" should be replaced by the simpler one of "number of chromosome arms" or "N.A." (fig. 3), which may be defined as "a measure of the number of chromosome arms in a given caryotype excluding only the minute short arms, which are at the limits of resolution by normal light microscopy, of acrocentric or 'telocentric' chromosomes." If such a definition as this is adhered to, then much of the confusion and subjective bias will be eliminated.

(*b*) Structural change not involving the centromere (fig. 4). Rearrangements of this type lead to alteration in chromosomal morphology without any concurrent alteration in chromosome number or N.A. The principle types are translocations and paracentric inversions. These will be directly detectable only by their pairing behaviour at meiosis in heterozygotes. Meiosis in translocation heterozygotes is likely to be abnormal leading to a breakdown in pairing and segregation, and therefore to some degree of semisterility. For this reason alone, unless these changes lead to gross heterosis, they are unlikely to be successful in a polymorphic population. However, should they become established as homozygotes, they will then breed normally and become subject to the same selective pressures as any other type of variation, and may establish themselves as variant caryotypes.

The Results of Chromosomal Change.

The results of chromosomal change can be analysed in two ways :—

(1) By inference from chromosome studies of closely related species. It is often possible to infer the types of chromosome change which have taken place during the course of evolution.

(2) By analysis of intraspecific chromosomal variation.

(*a*) Chromosomal polymorphism.

(*b*) Chromosome races.

(1) *Interspecific chromosome variation in mammals* (fig. 5) clearly shows the great variability in mammalian chromosome number. However, despite this apparent heterogeneous mass of data, a number of interesting points emerge :—

(*a*) The chromosome numbers of Marsupials are significantly lower than those of Eutherian mammals with a spread from $2n = 10$ to $2n = 28$. A distinctive peak occurs at around $2n = 14$ or 16. The range of diploid numbers in Eutheria is much more widely spread, ranging from 17 to 84, with peaks at 38, 42 and 60, each representing a definite group of animals. For instance, the Carnivora make up much of the peak at $2n = 38$, the Chiroptera and Insectivora at $2n = 42$, and the Ungulata $2n = 60$, these figures being the modal diploid number for each of these groups. In the Rodents, which are shown separately, there is a significant peak at $2n = 48$.

(*b*) A possible relationship between the diploid number and the N.A. for a single group of rodents, the Microtinae, is shown in fig. 6. The diploid numbers in this group vary from $2n = 17$ to $2n = 62$, a range of 45. On the other hand, apart from the two species with diploid numbers of $2n = 17$ both of which have an N.A. of 34, the variation in the N.A. is much less than the variation in the diploid number. The N.A. only varies from 46–62, a range of 16, with a mode at around 56. This suggests that the major component of variation in the chromosomal evolution of this group is of the fragmentation-fusion or "Robertsonian" type, accompanied, perhaps, to a lesser degree by inversions and other forms of structural change. The two species with 17 chromosomes clearly form a specialized group of their own, both are highly specialized for a fossorial existence, and in both the sex chromosome mechanism

	METACENTRIC	ACROCENTRIC	'TELOCENTRIC'
CHROMOSOME TYPE			
N.A.	2	1	1

FIG. 3.—The " Fundamental number ", or " Number of Chromosome Arms ".—N.A.

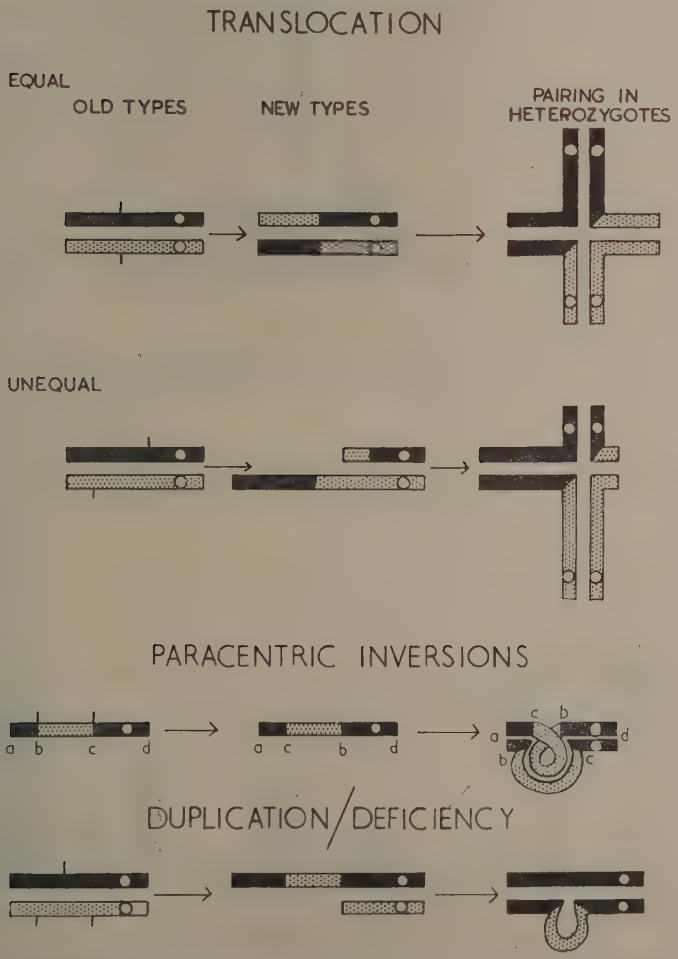


FIG. 4.—Chromosome rearrangements not involving an alteration in the position of the centromere.

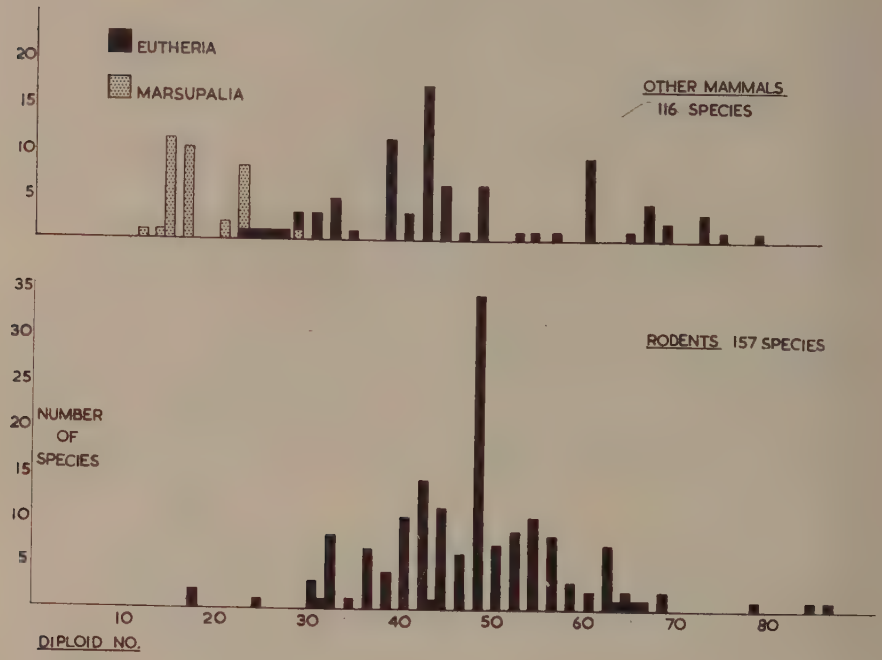


FIG. 5.—Histograms showing the distribution of the diploid chromosome numbers of mammals.

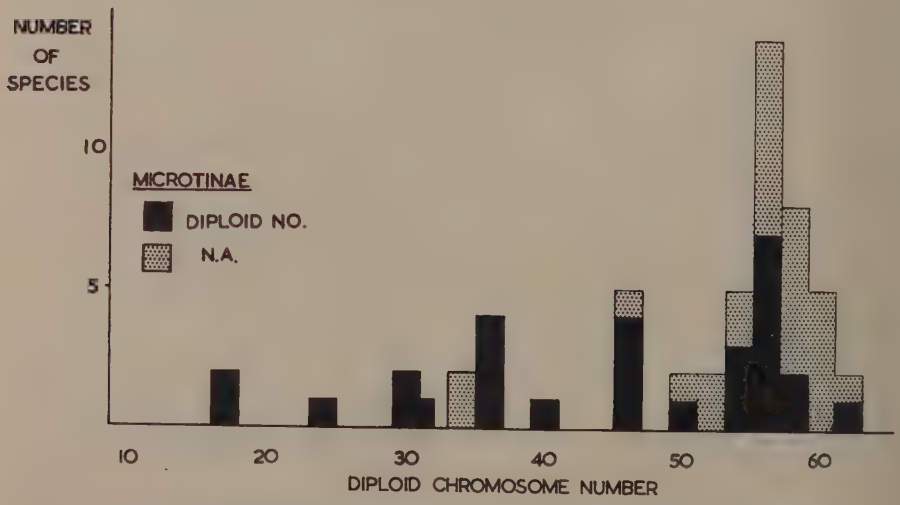


FIG. 6.—Histogram showing the relationship between diploid chromosome number and N.A. in the Microtinae (based mainly on the data of Matthey).

is aberrant. In the case of *Ellobius lutescens*, Matthey (1954*a*), has reported a diploid number of 17 in both male and female, without any apparent sex-determining mechanism. He has further suggested (1956), that only the females have functional gonads and reproduce parthenogenetically. In the other species *Microtus* (*Chilotus*) *oregoni* (Matthey, 1956*b*, 1957), the chromosome number is 18 in the ♀ and 17 in the ♂, suggesting that there is an X–O sex-determining mechanism. Matthey (1957), has suggested that this is an intermediate form between the genus *Microtus* and the genus *Ellobius* and the link by which *Ellobius* is connected to the rest of the Microtinae.

(c) *Polyploidy*.—The question whether polyploidy has played any significant part in mammalian chromosome evolution has been recently discussed (Sachs, 1952, 1956; Darlington, 1953; and Matthey, 1953, 1954*b*). Sachs (1952), attempted to show that the Golden Hamster, *Mesocricetus auratus*, arose as an allopolyploid hybrid from a cross between the Chinese Hamster *Cricetulus griseus*, and the European Hamster, *Cricetus cricetus*. This view was strongly supported by Darlington (1953). The evidence, summarized in fig. 7, suggests

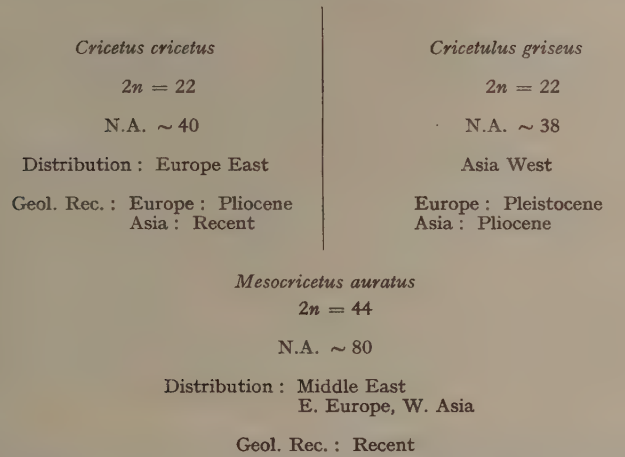


FIG. 7.—Diagrammatic representation of the evidence in favour of an allopolyploid origin for the Golden Hamster (*Mesocricetus auratus*). (After Darlington & Sachs.)

an apparent doubling of the diploid chromosome number and the N.A.: the geological record indicates that *Mesocricitus* is a geologically younger form than the other two species. Finally, *Mesocricetus* occurs in the geographical region where the distribution of the other two species overlaps. Matthey (1952, 1953, 1954), has rejected the polyploid hypothesis and suggested that the chromosome complement of *Mesocricetus* evolved by means of a number of pericentric inversions from a primitive caryotype consisting of about 48 acrocentric chromosomes. The caryotypes of *Cricetus* and *Cricetulus* are then supposed to have arisen from the chromosome complement of *Mesocricetus* by centric fusions between homologous chromosomes, accompanied by an extensive loss of centric fragments. The evidence for this hypothesis is no more conclusive than for the hypothesis of Sachs & Darlington. Table I shows the diploid numbers and the N.A. of the old world Cricetinae. Clearly there are three groups containing species with diploid numbers of, or approximating to, 22, 30 and 44 chromosomes. At first sight this suggests polyploidy.

TABLE I.—Cricetinae—Old World Hamsters. Chromosome data.

Species	2n	Approximate N.A.	Distribution
Cricetulus griseus	22	38	China.
Cricetulus migratorius	22	42	Russia.
Cricetus cricetus	22	38–40	W. Europe—Siberia.
Cricetulus triton	30	30 ?	China.
Mystromys albicaudatus	32	50	S. Africa.
Mesocricetus brandti	42	77–84	Caucasus.
Mesocricetus auratus	44	Ca. 76	Syria.

If so, then it is necessary to account for the survival of the two apparent triploids, and to be convinced that 22 is the primitive number for the Cricetinae in the face of evidence that the primitive or modal number for the Rodentia is nearer 48. We are left then with the situation that whether or not an isolated case of polyploidy has occurred in the evolution of *Mesocricetus* from the *Cricetus-Cricetulus* groups, it certainly does not appear to be the main factor in the chromosomal evolution of the Cricetinae. The available evidence (Simpson, 1945), suggests that the centre of evolution of this group was in the holarctic region with various branches spreading southwards from time to time as geological conditions permitted. From the primitive Hamsters of Europe and Asia evolved the modern genera, which are first recorded in the Pliocene era. It is uncertain whether *Mesocricetus* evolved later from these same primitive forms or whether it arose as an allopolyploid hybrid. A great deal of research, in particular a more detailed analysis of the chromosomes, and perhaps breeding experiments by means of artificial insemination, is needed before there is any hope of settling this question. The genus *Mystromys* is something of an enigma, being the only Cricetine in S.Africa, with no geological or other record to connect it to any of the other forms, and it is uncertain whether it is more closely related to certain S. American forms or to the old world Hamsters (Ellerman, 1941).

Intraspecific Chromosomal Variation.

(1) *Chromosomal polymorphism.*—Wahrman & Zahavi (1955 and per. comm.) reported variation in chromosome number in a population of *Gerbillus pyramidum* from the Negev in Israel. They found that the number of bodies observed at meiosis varied from 31 to 33 in different individuals, thus giving a variation in diploid number from 62–66. They also report individuals with trivalents at meiosis. The variation would appear to occur in two autosomal pairs and to be of the fragmentation–fusion or " Robertsonian " type, thus giving a possibility of seven variant caryotypes (fig. 8) within the population. Similar variation was reported by Sharman (1956) in 7 individuals of the common Shrew, *Sorex araneus*. A more detailed analysis of the situation in this species is now available (Ford, Hamerton & Sharman, 1957, and unpublished data). In this instance, three autosome pairs are involved. The chromosome number of approximately 100 shrews from seven localities in the British Isles has been determined, and found to vary between individuals from 21–27 in males, and 20–25 in females. The situation is complicated by the presence of a multiple sex chromosome mechanism, the males being XY_1Y_2 and the females XX (Sharman, 1956). The variable autosomes are pairs 6, 7 and 8 in order of decreasing length, and it is possible in good preparations to recognize all three pairs. In the present instance, 3^3 or 27 variant caryotypes are possible, of

which 19 have been observed. This variation is of the "fragmentation–fusion" or "Robertsonian" type, the N.A. always being constant at 40. Examination of a number of geographically separate populations shows that the frequency of the different chromosomal types varies from population to population, and further, that several of the populations examined show a high degree of homozygosity, suggesting perhaps a high rate of inbreeding, coupled with a rapid decline and subsequent rise in population levels from a relatively few closely related individuals.

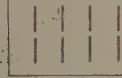
CHROMOSOME TYPES	2N	MEIOSIS
	62	31^{II}
	63	$30^{II} + 1^{III}$
	63	$30^{II} + 1^{III}$
	64	$29^{II} + 2^{III}$
	65	$31^{II} + 1^{III}$
	65	$31^{II} + 1^{III}$
	66	33^{II}

FIG. 8.—Chromosome polymorphism in *Gerbillus pyramidum* (based on the data of Wahrman & Zahavi).

(2) *Chromosome races.*—In their 1955 paper, Wahrman & Zahavi reported that *Gerbillus pyramidum*, besides being polymorphic, in one of its populations, also exists as entirely separate chromosome races occurring in separate geographical regions of N. Africa and the Middle East. The increasing chromosome number in respect of population samples collected in Algeria ($2n = 40$), Israel (coastal plain) ($2n = 52$), and Israel (Negev) ($2n = 62$–66), is related to a reduction in the number of metacentric chromosomes, whilst the N.A. remains virtually constant. This situation has apparently arisen by the stabilization of "Robertsonian" variants into definite and distinct chromosomal races. Taxonomically, such differences as exist between the six specimens examined from the three races are not such as would justify nomenclatural differentiation according to the normal criteria used in taxonomy (Morrison-Scott, 1955). A situation then exists in which isolation of polymorphic variants within a single inbreeding population has presumably resulted in the establishment of three distinct chromosome races (fig. 9).

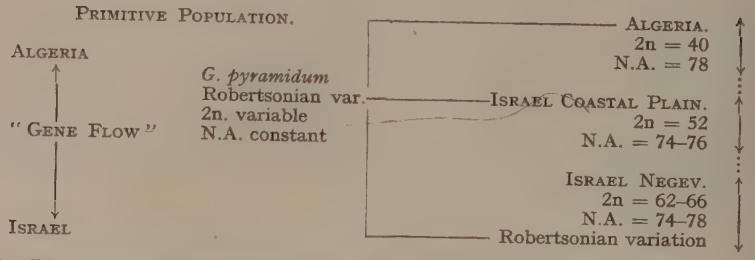


Fig. 9.—Diagrammatic representation of the origin of the three chromosome races in *Gerbillus pyramidum* (based on the data of Wahrman & Zahavi).

Zahavi & Wahrman (1956), report chromosome races of a different kind in the rodent genus *Acomys*. In two races, one from Cyprus and the other from Israel, these authors find the same chromosome number, $2n = 38$, the populations differing from each other in the number of metacentric chromosomes and in the N.A. The variation is thus probably due to pericentric inversions or translocations. Studies are at present being made on hybrids in order to determine the cause of this variation.

Chromosome races are suggested in a number of other groups (Table II). In all cases, however, this variation has been reported by different authors, and while undoubtedly some cases are based on fact, others are likely to be due to error, either of identification or observation.

Table II.—Possible existence of chromosome races in mammals.

Population	2n	Author
Sciurus carolinensis carolinensis	48	Cross, 1931.
Sciurus carolinensis leucotus	28	Koller, 1936.
Vulpes vulpes	34	Wipf & Shackleford, 1942.
	38	Makino, 1944.
Vulpes v. fulva	42	Wodsedalek, 1931.
	32	Bishop, 1942.
Talpa europaea	38	Koller, 1937.
	34	Bovey, 1949.

Discussion.

It is necessary to stress that the importance of the chromosomes lies not in their morphological but in their genetic character. The importance of chromosome change in evolution may then be summed up by one word, isolation. Blocks of genes are first isolated in the interchanged or inverted segments of the chromosome by a reduction in crossing over and recombination. Secondly, reproductive isolation may result from chromosomal rearrangements : breeding between individuals heterozygous for the rearrangement and normal individuals will be reduced. Thus the overall effect from the introduction of a rearranged caryotype into an otherwise normal population will be a reduction in " gene flow ". It is thus possible to envisage the formation of a new species as a result of genetic and reproductive isolation caused by chromosomal rearrangement followed by the action of natural selection on the rearranged genotype, leading eventually to phenotypic differences of a specific nature.

Morphological studies of the type reviewed here are of importance in so far as they are the only practical means of assessing the relative importance of the different types of change involved. Some idea of the genetic and cytogenetic changes which have occurred during mammalian evolution may thus be obtained.

Summary.

1. Recent advances in technical methods for the study of mammalian chromosomes are discussed. The relative simplicity and rapidity of modern methods is emphasized.

2. The concept that chromosome number must necessarily be constant throughout the range of a morphological species is considered and rejected. In consequence, the use of chromosome number alone is insufficient in comparative work. Future studies should deal in more detail with the morphological structure of the chromosomes.

3. The relative importance of aneuploidy, polyploidy, and chromosome rearrangement are considered in relation to the evolution of mammalian caryotypes. It is emphasized that no immediate relationship necessarily exists between chromosomal and phenotypic change.

4. Data available on the chromosome number in mammals and on the relationship between chromosome number and morphology both at the inter- and intra-specific levels suggests that chromosome rearrangements of the "fragmentation-fusion" or Robertsonian type are likely to be the commonest cause of variation between different mammalian caryotypes. Inversions seem likely to be of less importance in mammals than in other groups.

5. The evidence that allopolyploidy has occurred during the evolution of the old world Hamsters, is discussed. It is concluded that, although the circumstantial evidence put forward could be explained on this hypothesis, the question could by no means be considered settled. Further detailed morphological studies on the chromosomes are required, and it is felt that some attempt should be made to produce experimental hybrids and back-crosses for cytological examination.

6. The existence of polymorphic variation in the chromosomal complements of two distinct species of mammals is discussed. The existence of one of these species as three geographically isolated chromosomal races is also noted.

7. In conclusion, it is suggested that the major function of chromosome change is the introduction of discontinuities within an inbreeding population, leading to some degree of reproductive isolation. This in turn, through the action of natural selection on the altered genotypes, might lead to phenotypic differences of a specific nature.

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Chromosomes and Taxonomic Importance. By A. J. Cain, Department of Zoology and Comparative Anatomy, University Museum, Oxford.

That chromosomes are often useful in taxonomy is by now sufficiently evident. They can be of very great importance. But there has been little analysis of what is meant by taxonomic importance, and consequently of what precise contributions the study of the chromosomes can make to taxonomy.

The activities of the taxonomist can be broadly summed up as follows :—

(1) Identification.

(2) Recognition of forms below the species, and their proper allocation (classification of polymorphs, the sexes of the same species, stages in complex life-cycles, mutant forms, phenotypical variants etc.).

(3) Recognition of units of evolution (local populations, subspecies and species in sexually-reproducing organisms, clones and agamospecies in others).

(4) Brigading the forms recognized into larger groups as nearly as possible expressing the probable course of evolution.

The word *important* is used with reference to all these activities. Some of the meanings that have been attributed to it are as follows :—

(i) The more constant and conspicuous a character, the more important it is in recognizing again a particular form ; it is a good label, and useful for pure identification.

(ii) The more constant a character is, and the less subject to variation, the more useful it is in drawing up a description of a form.

(iii) The larger the taxonomic group throughout which a character occurs, the more important that character is taken to be.

(iv) The more a change in a character would affect the organization and mode of life of a form, the more important it is considered to be, since it is likely to remain fairly constant during evolution, and so provide a reliable guide to phyletic affinity.

(v) The more complex an organ, the less likely is it to have arisen more than once, and the more important is it for a phyletic classification.

(vi) Irrespective of the considerations in (iv) and (v), if a particular character is found to remain constant in a given phyletic line while others are changing it is important since it serves as a good recognition-mark for the members of that line.

(vii) Any evidence that two forms, although spatially able to do so, do not interchange genetic material in the wild, is of importance in establishing their biospecific distinctness.

(viii) Any evidence which shows that two or more forms can be found in the progeny of a single parent, or that one is converted into another in the course of a single life-history is of importance in sorting forms below the species level.

(ix) Any evidence which indicates the actual phyletic relationships of two

forms is of importance in making a phyletic classification. Such evidence includes the physical position of fossils in a series of strata, the geographical evidence that an enigmatic form is a peripheral subspecies of a widespread species, etc.

The first six of these meanings refer mainly to structural and other characters observable on isolated specimens, the remaining three to their behaviour, locality, or other properties not observable as parts of specimens. It may be said at once that since fresh material, on which alone chromosomes are observable, does not provide us with indisputable and complete phyletic lines, meaning (vi) is unimportant in this paper. Meaning (iii), moreover, is in effect merely an indirect method (much used when direct methods are not possible) of estimating importance in the sense of meaning (iv).

Now if we consider what evidence can be got from the study of chromosomes, we can see that they can contribute to several taxonomic activities.

It is well known that in some difficult groups, one glance at the chromosomes gives more certainty of the correct identification of the material than days of routine investigation. Mr. A. B. Acton gives in this symposium an example in which species of *Chironomus* are readily identified by means of their salivary gland chromosomes, but perhaps never invariably correctly on structural characters of the adults. Here the chromosomes with their different lengths, expansions in different places, and above all their fantastic multiplicity of bands of different intensities and spacings, provide such a wealth of characters that they can obviously be used in meaning (v) and in meaning (i). In spite of inversions and translocations, the characters of the chromosomes of each species can be clearly recognized, and the chances that an individual of one species could have independently acquired the characters of another is practically *nil*. And moreover, if two species are markedly similar in their chromosomal characters, by the argument just given it is reasonable to believe that they are phyletically closely related. The importance of the chromosomes as structural complexes in identification and in grouping species (activities (1) and (4)) has therefore exactly the same basis as does important evidence drawn from any other part of the structure of animals or plants (Cain, 1956). And when as is sometimes the case the chromosomes of a group are rather uniform and show virtually nothing of their structure, they may be of little use.

On the whole, chromosomes give little help in activity (2). What is needed here is to raise the progeny from a single individual, or to keep larvae until they become adult, or to rear sibs under controlled conditions. If a given sample of individuals is believed to contain a mixture of species, then a study of their chromosomes may allow them to be sorted out, and even for particular larvae to be assigned to the same species as particular adults ; but the use of the chromosomes here is purely for identification (activity (1)).

In activity (3), however, chromosomal studies can be of great use. If two forms are found to have markedly different chromosome complements, it is highly unlikely that they will produce fertile hybrid offspring in the wild ; such evidence is therefore important in sense (vii). However, it must be realized that it is only substitute evidence. Wahrman & Zahavi (1955) have shown variation in chromosome numbers apparently within single populations of sexually reproducing rodents. We do not know how different two chromosomal complements must be to be incompatible with the production of fully fertile hybrids. In general, the evidence required is that the two forms under investigation do not exchange genetic material in the wild, whether or not they can as far as chromosomal differences are concerned. This can be finally determined only by examining wild populations for successful hybridization, and chromosomal evidence, although often of great weight, is only a substitute (Cain, 1956). But if one form appears to be a diploid and another a tetraploid derived

from it, then one can say that infertile triploids will result from any cross, and in the absence of some form of vegetative reproduction will produce no offspring. Here, a mere examination of the chromosomes has almost the weight of an actual demonstration by means of breeding data.

A study of chromosomal behaviour may also show that a form is parthenogenetic or bring to light other processes that allow us to classify it as an agamospecies. In fact the revelation of the breeding system may be the most important evidence for activity (3) that the chromosomes can provide.

In activity (4) chromosomes help in two ways. If they form highly complex systems of usable characters, then as already mentioned, they have the same use as any other structures in the production of a supposedly phyletic arrangement. But in addition they can provide direct evidence of the course of evolution. The recognition of a tetraploid identical in other respects with a known diploid allows us at once to place that tetraploid as a derivative of the diploid, since the process of reducing chromosome numbers by losing a whole set at a time seems a most unlikely one. (But no doubt it is not absolutely impossible). Again, when the detailed structures of chromosomes can be used taxonomically, as is the case with the salivary gland chromosomes of Diptera, and lamp-brush chromosomes, it may be possible to show that a chromosome in a particular population has undergone two inversions of which one must be later than the other since it involves a part of it. Any such evidence is important in sense (ix) and of considerable interest to biologists generally. Unfortunately the dating of the successive inversions may not be simple, as the discussion between Mayr & Epling shows (Mayr, 1945), and in general this sort of chromosomal evidence is likely to relate only to populations of the same species or of closely related species.

The usefulness of chromosomes can be well illustrated by recent work on the chromosomes of earthworms. These have been explored especially by Omodeo (e.g. 1952, 1955) and Muldal (1952) working on the Lumbricidae; Christensen & Overgaard Nielsen (1955) have made a beginning on the taxonomically very difficult Enchytraeidae. Of the twenty-three species examined by Muldal, six are parthenogenetic and almost certainly polyploid, and must be regarded as agamospecies. Omodeo describes triploid *Allolobophora caliginosa trapezoides* from several places in Italy, and tetraploids from near Naples. Christensen & Overgaard Nielsen report that the currently recognized species *Henlea* (*Michaelseniella*) *nasuta* seems from their material to be a good species, chromosomally homogeneous, while *H.* (*H.*) *ventriculosa*, an equally well-defined form has $n = 17$, 34, or 60–70. Moreover they report for the first time, on chromosomal evidence which they carefully point out is indirect, the occurrence of parthenogenesis in the Enchytraeidae. The bringing to light of these and many other such facts shows how necessary it is that the ordinary taxonomy of the Oligochaeta should be supplemented by cytological study whenever material permits.

However, there are certain difficulties in the use of chromosomes, which must also be mentioned. Perhaps the most important is that since we have no precise information on the exact significance of the chromosome number in any species of plant or animal, we have no idea at all of what selective pressures are likely to affect it, nor, therefore, of what circumstances are the most likely to favour a change in it. Consequently we have no estimate of the likelihood of convergence in it. Many different organisms, no doubt, do have the same diploid number, but since they are obviously different on ordinary taxonomic evidence, no confusion is caused. But within a closely related group in which the chromosomes are small and little more than their number has been observed, it may be that different species have arrived independently at the same number, and the taxonomist must be wary in his interpretations. The most favourable

situation is when the structures of individual chromosomes can be investigated, and a vast number of characters can be used. The chromosomes are only one among the many structural systems possessed by organisms, and may be subjected to selection pressures not experienced by other structures. There is no need to suppose that complex chromosomal systems are necessarily correlated with a complexity of macroscopic structure, nor that species very similar in their general morphology must have very similar chromosomes. In assessing overall taxonomic affinity, the chromosomes as such can have no greater importance than any other structural system. Their importance, in sense (iii) above, depends on their covariation with all other characters (Cain, 1954, p. 25).

Moreover, even when a large number of chromosomal characters can be observed, there is still often room for considerable uncertainty about their significance for phylogenetic conclusions. Muldal (1952) has made some interesting suggestions about the evolution of chromosome numbers in the earthworms, but it is doubtful whether they can be regarded as acceptable. On the basis of his own counts of numbers in 30 forms all from the Lumbricidae, and of 14 others from various oligochaetes, and a comparison of these with only 19 species of polychaetes, he says that it is reasonable to assume that there has been a general trend towards increased numbers in the terrestrial annelids. This is surely not an adequate survey to base such a conclusion on ; it omits the terrestrial Enchytraeids and the whole of the Moniligastrids, Megascolecids and Eudrilids, and its coverage of the polychaetes is hardly sufficient. Christensen & Overgaard Nielsen's numbers for their Enchytraeids certainly overlap at the lower end of their range with the highest numbers Muldal quotes for the polychaeta. Moreover, although the oligochaetes certainly seem to have arisen from polychaete-like ancestors, it is very doubtful whether any group of present-day polychaetes are really close to those ancestors in any way, chromosome number included. Christensen & Overgaard Nielsen also criticize Muldal's assumption on the basis of the chromosome numbers known to him, that the diploid species of Lumbricidae are really old tetraploids. However, they themselves say that the family Lumbricidae is one of the youngest families, and so it is of interest that its generic limits are badly defined (as indeed they are) and that so far only five haploid numbers (as against nine in the much older family Enchytraeidae) have been reported for them. I am afraid that earlier taxonomists are responsible for these relative ages of the two families, and there is no more basis for them than for Muldal's assumption that the chromosome numbers of present-day polychaetes will be like those of the ancestors of the oligochaetes. In general, the orthodox taxonomist, saddened and in part disillusioned by the failures and uncertainties of phyletic interpretation of more familiar evidence, can be of considerable use to the purer cytologist by leading him away from many pitfalls of interpretation.

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EFFECTS OF OUTCROSSING ON THE CHROMOSOME NUMBER IN VERTEBRATES. By DR. M. FISCHBERG.

The percentage of embryos (F_1) from matings within an inbred line (mice) was found to be negligible. Heteroploid embryos occurred, however, if individuals from different inbred lines were crossed. In Amphibia the percentage of young with abnormal chromosome number increased with increasing genetical variation of their parents. A hypothesis is put forward which tentatively proposes a new mechanism in the evolution of chromosome numbers in animals.

A CYTOLOGICAL COMPARISON OF NEARCTIC AND PALAEARCTIC REPRESENTATIVES OF *Chironomus tentans* (DIPTERA). By A. B. ACTON, Department of Zoology, University College of North Wales, Bangor.

It is thought that most species arise by the gradual accumulation of minute changes ; the final result may be that the two groups of organisms become reproductively isolated, but this is by no means a generally accepted criterion of what constitutes a species. Unfortunately, there have been very few opportunities to study these changes, mainly because the evolutionary process is so slow, but partly because it is difficult to decide how much a particular character is affected by factors which are inherited, and how much by factors which are not. Thus the wings of the flies in one of two separate populations which are destined to become specifically distinct may in time become longer, but the length of the wing may, for example, also be influenced by the amount of food the larva has been able to eat. Such a character, unlike some, is capable of infinitely small changes which can in theory be detected, but it is doubtful whether it will ever be possible to discover every factor which contributes to a given variation. If it were possible to recognize and ignore all the extraneous variables, leaving only the fraction which is due to the process of speciation, it might be possible to estimate, by comparing the same character in closely related species, how much progress a given population has made to becoming a separate species.

Perhaps the only character which can satisfactorily be used for this purpose is the banding pattern of the giant chromosomes, though this is confined to members of the Diptera. The banding patterns are never used *as such* by the animal, and it is therefore hardly likely that patterns in unrelated animals will come to resemble each other because these animals use some part of their environment in exactly the same way ; in short, the banding patterns will not be subject to evolutionary convergence. Apart from well understood differences, nearly always inversions, the characteristic succession of dark and light, thick and thin, bands looks the same in the giant chromosomes of all the animals from a single breeding group : the chromosomes of offspring are derived directly from the chromosomes of the parents by meiosis and mitosis. There are of course slight variations in the appearance of individual bands, and in the degree to which a chromosome stains, but these variations are as easily allowed for as the fact that some cats are black, and some yellow, but all are nonetheless cats. However, it is the inversions which are of particular interest from the taxonomic point of view.

The members of each homologous pair of giant chromosomes in a nucleus lie side by side in close contact, so that if one of them is different from the other, this is easily seen. When one of the chromosomes has a section which is inverted, the pair still lie side by side, but a loop is formed in the region of the inversion. Complex rearrangements of the chromosome by successive inversions are recognized by the complex pairing-loops which they form.

Each chromosome of *Chironomus tentans* has a banding pattern which occurs more frequently in a population than the others, and so may be used as a " standard " or reference pattern. The standard patterns which are found in Sweden, Germany and Austria (Beermann, 1955), and in the British Isles (Acton, 1957) are identical. Furthermore, many of the inverted sequences in these localities are also identical ; and an inverted sequence which is found in one region only is always found with a banding pattern which occurs in all the other regions.

Only one species, *C. pallidivittatus*, is known to be closely related to *C. tentans* ; *C. pallidivittatus* occurs in Europe, but it is not as widespread as *C. tentans*. Since there are morphological differences between the imagines, and, further, since populations of the two species are able to live together in the same ponds and yet maintain their independence in the face of occasional hybridization (Acton, 1957), there can be no doubt that these are indeed true species. The banding patterns of *C. pallidivittatus* resemble those of *C. tentans* in many respects, and in fact only differ from them by inversions. As might be expected, since hybrids are occasionally found in natural populations, it is possible to obtain hybrid larvae under experimental conditions. Beermann (1955) observed some 50 copulations between members of the two species, but about 90 per cent of these were sterile. Even when such inter-specific crosses were successful, only a small fraction of the eggs were fertile : fewer than 5 per cent of the eggs were fertile in four of the egg masses, and in three others the fractions were 25 per cent, 40 per cent and 70 per cent. Thus not only is there a large number of unsuccessful matings between the species, but there is also a greatly reduced fertility of the matings which are effective, and it is easy to see how these factors would suffice to keep the species apart.

None of the chromosome banding patterns of *C. pallidivittatus* is identical with any of *C. tentans* ; the inversion loops which are seen in the rare hybrids are never seen in the chromosomes of the parent species. This is just what might be expected of the banding patterns in species which have not exchanged genes for a considerable time.

The stage is now set for the introduction of a third group, the Canadian representatives of *C. tentans* (samples were taken from Toronto, Ottawa, Montreal and Churchill). The banding pattern of chromosome 2 (the second longest) of Canadian *C. tentans* is different from that of European larvae ; again it differs by inversions, and none of the alternative patterns of this chromosome in Canada is found in Europe, and vice versa. Chromosome 3 in Canada differs by the lack of a " puffed " region, and by the presence of an additional band near its centre. In neither chromosome is there a pattern which is found on both sides of the Atlantic, and in this respect the differences are comparable with those which are found between *C. tentans* and *C. pallidivittatus*, and so might be judged of " full specific rank ". However, this is not true of chromosomes 1 and 4, since there are banding patterns of both which occur in Canada and Europe. Furthermore, there are banding sequences in Canada which are derived from the patterns that are the same in both regions, but these sequences have not been seen in Europe : and conversely there are patterns in Europe which were not found in Canada.

Though it is often possible by examining their giant chromosomes to identify the locality from which a large sample of *Drosophila pseudoobscura* was taken, this cannot in general be done with a single fly (see Dobzhansky, 1951). By

contrast, a single *C. tentans* larva can be seen at once to have come from Canada (or Europe). There is no lack of evidence that the Canadian and European populations of *C. tentans* have been genetically isolated for a long time.

Externally, there are no detectable differences between the larvae from the two continents, but there are slight, perhaps real, differences between the imagines (I made only 5 comparisons). I was able to make only two crosses between an imago from England and one from Canada. Both were successful and, as far as I could see, all the eggs were viable. Thus there appears to be no reproductive isolation, though this might have been expected from the chromosomal differences. However, if populations are completely separated geographically, there is no reason why reproductive isolation should be of any advantage, and so be selected for.

If the Canadian and European populations of *C. tentans* are incipient species, the question arises which will come first: the disappearance of the banding patterns that are shared, or reproductive isolation? And will both be preceded by the appearance of striking external differences? There seems to be no simple answer to the question when separate species will emerge.

The imagines of *C. tentans* are short-lived and the eggs must be kept moist if they are to survive. Further, the larvae are apparently found only in ponds of a certain type, so that even if the hazards of migration are overcome, the chances of coming upon a suitable pond seem to be slight. This view is to some extent supported by evidence that populations in England even a mile apart may have significantly different frequencies of chromosome banding patterns (Acton, 1957). For these reasons the original populations of *C. tentans* are much more likely to have migrated across the Bering Strait than across the Atlantic (accidental transport, though remotely possible, would have been so recent that it can affect the argument little; there is certainly no evidence of it). *C. tentans* occurs at Churchill (lat. 59° N.) so that there is no reason why there should not still be a certain amount of migration across Asia. Samples of larvae from Alaska and Russia would give the answer. If there is no migration now, it must have taken place when conditions were different: there is a chance that it may be possible to arrive at a rough estimate of the length of time which has elapsed since the banding patterns of *C. tentans* in Canada and Europe were perhaps the same.

The banding patterns of the giant chromosomes are an ideal character with which to detect even quite small changes that have been brought about in the course of evolution. Though a great deal of information can be obtained by this method, there seems little hope of arriving by its use at a more useful definition of the species than now exists. Though it is possible to detect minute differences between the giant chromosomes of different larvae, it may still be no easier to decide the taxonomic status of the animals concerned, and it will be necessary to appeal to the "competent taxonomist".

I am indebted to the Department of Botany in the University of Toronto for their generous hospitality, and to the Royal Society and Nuffield Foundation for a bursary.

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Chromosomes and Fern Phylogeny. By Irene Manton, F.L.S.

The bearing of recent cytological work, mainly on tropical fern genera, on current views of fern phylogeny.

The Cyto-taxonomy of a Tropical Fern Complex (*Pteris quadriaurita* complex). By T. G. Walker.

The large complex species centred on *Pteris quadriaurita* Retz presents great taxonomic difficulties. It is proposed to show how cytology and experimental methods have led to an understanding of some of the underlying causes of the taxonomic complexity of this group of ferns as represented in Ceylon. The results will also be discussed in relation to the behavour of the plants as studied in the field by the speaker.

Cytotaxonomy of the Rostrate Violets. By D. H. Valentine, F.L.S. (Durham University).

The Rostrate violets, which form a subsection of the section Nomimium, are defined taxonomically by their style characters and caulescent habit. There are about 35 species, widely distributed in the temperate regions of the northern hemisphere; they are divided into 3 groups, which differ mainly in habit, viz .:

(i) *Mirabiles*, with basal rosette, acaulescent in spring, later becoming caulescent (2 spp.).
(ii) *Rosulantes*, with basal rosette, caulescent (c. 22 spp.).
(iii) *Arosulatae*, lacking rosette, caulescent (c. 10 spp.).

About twenty interspecific hybrids (mostly highly infertile) are known in nature, and many of these have been synthesized (by various workers). As these hybrids link the 3 groups, it is likely that the Rostratae as a whole are part of a single comparium. This comparium is very large, as Gershoy (1934) was able to make hybrids between the rostrate species *V. riviniana* and members of three other subsections (Stolonosae, Uncinatae and Boreali-Americanae); but these hybrids are difficult to make and rarely or never occur naturally. Thus the hybridization experiments provide some confirmation of the validity of the subsectional classification. Further support is provided by chromosome counts, summarized in Table I. All species so far investigated have a basic number of 10; (*V. lactea*, with $2n = 58$ (Moore, 1957) may be regarded as a subhexaploid).

There are many species not represented in Table I, e.g. these found in western Asia and Siberia; but the data as they stand indicate that the group has had a long evolutionary history, and that there has been extensive gradual-speciation.

The Arosulatae are not found outside Eurasia; in Japan and E. Asia only diploids are recorded, but in W. Europe there is a polyploid complex, of which *V. canina* is the most widespread member. There is evidence, from studies of

TABLE I.—Chromosome numbers of Rostrate Violets.

Data for N. American and some European species from Clausen (1929) and Gershoy (1928, 1934) and for Japanese species from Miyaji (1929); see also Valentine (1950). Arosulatae are italicized, and Mirabiles are bracketed.

	2*n*	4*n*	c. 6*n*	c. 8*n*
North America	rostrata conspersa labradorica striata adunca walteri	howellii	—	howellii
Eurasia	rupestris reichenbachiana (mirabilis) *stagnina*	riviniana *canina* *pumila* *elatior*	*lactea*	—
E. Asia and Japan	*micrantha* *thibaudieri* *raddeana* grypoceras faurieana sachalinensis rostrata obtusa	—	—	—

meiosis in interspecific hybrids, that *V. riviniana* and *V. canina* have one genome in common, and that genomic formulas can be written as in Table II.

TABLE II.

	Rosulantes	*Arosulatae*
Diploid	*V. reichenbachiana* A	*V. stagnina* C
Tetraploid	*V. riviniana* AB	*V. canina* BC

If the Rosulantes and Arosulatae come from a common stock, it is possible that the species with the B genome, which is not known at present, belonged to this stock.

The Mirabiles form a small, very distinct group, with a wide Eurasiatic distribution; they probably diverged early from the other groups.

The Rosulantes have a circumpolar distribution. One of the most interesting species is *V. rostrata*, which belongs to the large group of plants which has a disjunct distribution in eastern Asia and eastern North America. It thus probably formed part of the early or mid-Tertiary flora of the northern temperate forests. Gershoy (1934) showed that *V. rostrata*, *V. conspersa* and *V. striata* belonged to the same coenospecies (they could be linked by partially fertile hybrids), and also that these species probably had no genome in common with the European tetraploid, *V. riviniana*; (30 univalents at meiosis in *V. striata* × *riviniana*). These data may be taken to indicate that the primary evolutionary radiation of the Rostratae probably occurred in early Tertiary times, and possibly in eastern Asia. The number of species existing in this area at present is comparatively large, but their relation to the European and N. American members of the group has not yet been experimentally investigated; nor is anything known of the cytology or hybrids of such species as *V. mauritii*, which extend across Asia, partially bridging the gap between Europe and Japan.

Attention may finally be drawn to two other outstanding problems. The first concerns *V. howellii*, an endemic species of the western U.S., which was found by Gershoy to have both tetraploid and octoploid forms. The second concerns the taxonomically closely related species *V. rupestris* (which extends across Eurasia) and *V. adunca* (which extends across N. America); the relationship between these species and the rest of the group has yet to be determined.

List of Species of Viola mentioned in the Text

adunca Sm., *canina* L., *conspersa* Reichb., *elatior* Fries., *faurieana* W. Becker, *grypoceras* A. Gray, *howellii* A. Gray, *labradorica* Schrank, *lactea* Sm., *mauritii* Teplouchow, *micrantha* Turcz, *mirabilis* L., *obtusa* Makino, *pumila* Fries, *raddeana* Regel, *reichenbachiana* Jord., *riviniana* Reichb., *rostrata* Persh., *rupestris* Schmidt, *sachalinensis* Boiss., *stagnina* Kit., *striata* Ait., *thibaudieri* Franch. & Sav., *walteri* House.

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PRESIDENTIAL ADDRESS

Palaeobotany and the Evolution of the Flowering Plants.

By H. Hamshaw Thomas, M.B.E., F.R.S.

In my address last year I dealt with some of the ideas which have played a considerable part in the discussions about the evolution of the flowering plants. To-day I wish to examine another aspect of the problem.

The concept of organic evolution originated as a philosophical notion. It was a mental concept which sought to explain the existence of the multitude of living forms by reference to a series of supposed historical events which would account for many of the problems in the structure and distribution of plants and animals. There were many reasons for thinking that events of the kind postulated must have occurred, but there was little or no actual historical evidence showing that modern organisms had descended from simpler ancestral forms. The study of the evidence provided by the fossil remains of plants and animals thus became of supreme importance in the discussion of evolutionary problems.

For a long time the interpretation of the geological record presented enormous difficulties. The evidence was very fragmentary and incomplete, it was full of discontinuities, and the changes in form that could be seen appeared much too slow in relation to the period of time believed to be available. But during the past thirty years, the historical picture has been completely changed by the realization that the earth is very much older than was thought.

Towards the close of the nineteenth century physicists had approached the problem of the age of the earth from several aspects. From their observations and calculations Lord Kelvin had made an authoritative statement that the earth could not have supported organic life on its surface for more than 20 million years. Geologists, from a consideration of the thickness of sedimentary rocks and of their present rate of deposition, had demanded very much more time, but neither party had any idea of the internal sources of energy now known to us, or of the mode of dating rocks now universally accepted.

To-day we have good evidence of the presence of filamentous organisms in Precambrian rocks which may be between one and two thousand million years old, and there were highly organized vascular plants in various parts of the world some 300 million years ago. This very great extension of the time scale completely alters our ideas on the rate of evolution, and on the significance of the fossil record as a real historical document.

In spite of the very great increase in our knowledge of the plants of the past which has occurred during the past sixty years, we seem to have made little progress in unravelling the problem of the evolution of the Flowering Plants. It is widely held that the fossil record provides no assistance to the understanding of this problem. We know that the angiosperms became widespread in the world during Cretaceous times, some 100 million years ago, but we do not know where they came from, since they appear to be unrepresented among the world's floras of a previous date. But we may have been expecting too much. We have really no idea of the appearance of the most primitive angiosperm. We can be fairly certain that it did not resemble the conceptual *urform* of the idealistic morphology, and it seems unlikely that its leaves had the nervation characterisitc of modern dicotyledons. We may well have found examples of the ancestors of the angiosperms without knowing it. We need to sift our knowledge of pre-cretaceous seed plants and to ascertain if any of them show evolutionary trends towards the structures now found in the living forms of flowering plants.

It must be remembered that the historical approach to the study of plant evolution has much in common with the work of unravelling the problems of human history. Very often the historian has no written records of the period he is studying, such for example as the pre-Roman history of Britain. He goes to work by piecing together the information derived from the excavation of ancient towns, buildings or camp sites ; he takes into consideration old legends, the inscriptions on coins, and material finds of many kinds, as well as geographical considerations. And in time he is able to reconstruct a probable account of a long series of events. Without any direct evidence, but by assembling many disconnected facts, a coherent story is built up, and it is recognized that this story is provisional and liable to be emended as fresh evidence becomes available.

In the same way the student of plant evolution has at his disposal a very large amount of information relating to the plants which have flourished on the earth during the past 300 million years. Much of it seems, at first sight, quite disconnected, with no bearing on the history of the flowering plants, but from it we may learn much concerning the history of plant form, and about the slow changes in structure which led to the appearance of organs like those in modern plants. Critical consideration of the facts in their chronological order enables us to form some picture of probable evolutionary history of the largest group of forms in the present vegetation of the world, even though it is likely that this picture is only provisional.

When dealing with the fossil record of plant life on the earth we must always remember that the examples of ancient plants known to us represent only a very small fraction of the vegetation of land areas. Fossil plants are found in sedimentary rocks only if their organs had the chance of falling into aseptic mud in some slow-moving stream or lake or estuary. They had to be sealed up in the mud before they decayed. Occasionally living plants, or the plant debris on a swamp or forest floor were overwhelmed by water containing a high percentage of mineral substance in solution. Such solutions of calcium carbonate, silica or pyrites, could penetrate the greater part of cellular structures and solidify, leaving the plant organ embedded in a crystalline mass. It is by the discovery and study of material preserved in this way that we learn

about the anatomical structure of many ancient forms, but this petrification can never have been a common process. I doubt whether at the present day one hundredth of one per cent of living genera are in the process of being preserved as fossils, although it is possible that at some periods in the past the conditions for preservation may have been more favourable. In any case the plants growing on the fringes of estuaries, lakes and rivers would have a much greater chance of being preserved than those growing on dry ground at some distance from the coast, or from large lakes or rivers.

In many rocks we find well-preserved remains of the spores or pollen grains of the plants living in the vicinity at the time when those rocks were formed ; when these spores are extracted and examined we always find that many more kinds can be recognized than the number one would expect if they only came from the plants whose macroscopic remains are preserved in the same sediments.

We must also remember that there are large tracts of the earth's surface which have never been carefully examined by palaeobotanists. New forms of plants are constantly being discovered, and there can be no doubt that many more have never yet been seen by man. This is especially true for Africa and South America.

But although we cannot expect to find regular series of forms showing gradual transitions from one type of structure to another, it is easy to undervaluate the fossil material. We already possess samples of the vegetation of moist habitats from each of the major periods in the earth's history since the close of Silurian times some 300 million years ago. Some of these samples are small, but others contain several hundred forms, and probably include representatives of most of the major groups alive at the time. The evidence enables us to form well-founded opinions about the general trends in the evolution of a number of plant groups, and it proves that in several characters there was parallel evolution in unrelated races. Some of this evidence is relevant to the problem of the angiosperms, but the material must be viewed in its chronological sequence, and from an objective and materialistic standpoint.

I spoke last year about the inadmissibility of ideas derived from the old idealistic morphology, and I referred to the probability of a material difference between the vegetative and reproductive parts of plants. The fossil evidence shows quite clearly that the spore-bearing organs were not in the first instance leaves adapted for the functions of reproduction. In most of the earliest land plants known to us the sporangia were produced singly or in groups at the tips of branches, and not on leaf-like structures ; in many of these forms there were in fact no leaves. In the Upper Silurian Baragwanatha there were awl-like leaves, but the sporangia occurred on the stems between them. Psilophyton and Asteroxylon had small spine-like leaves on the lower parts of their branching stems, but the branches which terminated in sporangia were naked and slender. From rocks of a somewhat later date we find plants with much greater vegetative differentiation, but here again the sporangia were borne on slender branches, though sometimes these terminated portions of the plant body of a frond-like form. Thus the historical evidence agrees with the concept of a physiological distinction between vegetative and reproductive structures, and gives no support to the notion that all the reproductive structures in land plants were originally borne on sporophylls. The term sporophyll should therefore be discontinued or replaced by sporangiophore. It becomes highly probable that flowers originated from groups of sporangia and not from collections of fertile leaves.

Soon after the discovery of the Devonian plants, which were named by Kidston & Lang the Psilophytales, botanists tended to think that this group represented the ancestors of all the land plants of later times. But in 1954 Prof. Suzanne Leclercq pointed out that this group contained forms with very

different structure and probably included two main types, equal in importance to the Lycopsides and Pteropsides, rather than a series of convergent ancestral forms of these groups. Her argument rests on good evidence, and I think that it may well be extended. The vegetative structures of these early forms are so diverse that they can scarcely be regarded as closely related. The possession of terminal sporangia, which unites them, is probably not an exceptional feature denoting their common origin, but a primitive feature derived from their ancestors in an algal stage and retained in parallel evolution. There can be no doubt that parallel development has been of constant occurrence. The chief classes of Pteridophyta have been distinct from very early times, the similarities in their structure and reproduction are likely to be the results of parallel evolution. The seed habit has originated in more than one group of plants. Some of the tree Lycopods of the Carboniferous period produced integumented megasporangia, which were seeds in the biological sense, and fossils of the same age show that the Cordaitales had seeds which were anatomically different from the seeds of the pteridosperms. From the point of view of genetical relationships, the different classes of modern gymnosperms are not related plants, but forms at a common stage in evolution. It may well be that angiospermy also represents a stage in the evolution of plants that are not closely related, but here angiospermy is, as far as we know, accompanied by the remarkable process of double fertilization, which may be a more rigid proof of affinities.

It would be easy to cite many other instances of parallel evolution in the structure of the members of unrelated genera as shown by the historical records. We must therefore recognize that the changes which have taken place during the history of one group of plants may well have also taken place in another group living under comparable conditions. This consideration should be remembered when we discuss the possible ways in which the closed carpels of the angiosperms could have arisen. The valuable researches of Prof. Joseph Doyle on the pollination mechanisms in the Coniferales have shown how in this group there seems to have been a progression from primitive gymnospermy to the condition seen in Araucaria, Saxegotheca and Eutsuga where the pollen grains germinate at some distance from the micropyle and produce a long pollen tube which finds its way to the ovule. Dr. Mary Calder has pointed out there seems to be no reason why the mechanism of pollination and fertilization in the Caytoniales and the angiosperms should not have developed in a similar way.

The fossil record shows that since Devonian times the plants with woody stems, large fronds or leaves, and seeds, were distinct from the forms with small closely crowded leaves or from types with strap-shaped leaves having parallel veins. We find a succession of leaf forms in successive strata which make it highly probable that the leaves of the modern dicotyledons originated from branch systems produced laterally on relatively slender stems, and becoming progressively better suited for the work of photosynthesis. In the Middle Devonian they were repeatedly branched at frequent intervals, and their cortical tissues were slightly expanded. At a later date they became more varied in form. Some of the ultimate branches coalesced to form narrow pinnules, others were united at the base but free above ; in some, fan-shaped pinnules were evolved, or slightly elongated structures in which the original branches were represented by the veins with an unequal amount of growth. Many of these fronds closely resembled the fronds of ferns, and for that reason they were formerly believed to be the remains of true ferns. We now know that some of them were in fact the fronds of ferns, but most of them belonged to the seed plants which Scott and Oliver named the Pteridosperms. In the Upper Carboniferous period the pteridosperm fronds tended to become larger and more compact. Their differentiation into petioles or pinnae-axes with support-

ing and conducting functions, and pinnae or pinnules with photosynthetic functions, was more complete. The types resembling a system of flattened branches became infrequent. In some genera the nervation of the pinnules became reticulate; the frond segments were less separated, and some forms, like Gigantopteris, show an outline not unlike that of a dicotyledonous leaf. Formerly little was known about the plants which bore these leafy structures but during the past sixty years a considerable amount of information has been obtained about their stems and their reproductive structures. Scarcely a year passes without some additions to our knowledge of the group. We know that it contained a large number of forms of varied structure; it was world-wide in its distribution, and it did not become extinct until the Cretaceous period, if indeed it is not represented to-day by *Gnetum* and *Welwitschia*. In my view it is most probable that the flowering plants sprang from some of the earlier members of this group. Having flourished on the earth for at least 200 million years the pteridosperms merit close scrutiny to see if the forms already discovered had any characters comparable to those of the modern angiosperms.

Most of our knowledge of these plants comes from the study of isolated organs, sometimes with their anatomical structure preserved, but more often found as compressions in shale which show only a few of their characters. In one or two instances it has been possible to effect an almost complete reconstruction of the original plant by piecing together the separate parts, but in very few species can we obtain any accurate idea of their original size and habit. In no case can we point to a genus or species and say "this must be an ancestor of the angiosperms", but in the group as a whole there are many structures which seem significant, and are worthy of close consideration in relation to their place in the historical sequence.

In general habit the late palaeozoic pteridosperms seem to have been mainly shrubs or small trees with slender stems, but in the Permian rocks of Saxony there are some forms with massive trunks bearing huge leaf bases, a little like those of some palms. Certain types had axillary branching. A considerable series of petrified stems from rocks of ages between the Middle Devonian and the Permian shows that their axes had secondary wood together with the ancient type of centripetal xylem. There is evidence of the gradual loss of this old type of wood whose capacity for water conduction was limited. A similar loss of centripetal xylem occurred in the Conifers and the Equisetales. The earlier stems contained a single cylinder of wood, as in most of the dicotyledons, but several of the later genera show that the single cylinder was replaced by two or three smaller cylinders, or by a complex mass of vascular tissue with anastomosing strands.

Evidence that the fronds arose from specialized branch systems is provided by several of the early forms whose structure is preserved. The conducting tissue supplying the fronds came off as a single strand from the stem stele and sometimes grew into a small replica of the latter. It left a simple gap in the woody cylinder of the stem. This mode of origin of the leaf traces was very similar to that seen in those dicotyledonous stems believed by Dormer to show the most primitive type of vascular arrangement. A short time ago Prof. Andrews investigated the details of the structure of the secondary wood in several of the pteridosperm stems. He found that in several respects they were comparable with the stems of modern dicotyledons. They had numerous conspicuous medullary rays of considerable height and heterogeneous structure, together with a few low uniseriate rays. The tracheids generally show multiseriate bordered pits, with indications of their derivation from broad scalariform pits. There were, of course, no vessels, but the tracheids were very long, often reaching 24 millimetres in length. An interesting structural detail of these stems is that they usually show well-developed mechanical tissue in their

cortex, which was often closely similar to the strengthening tissues of some modern flowering plants, especially among the monocotyledons.

During the past 40 years much evidence has accumulated about the reproductive structures of the pteridosperms, the significance of which does not seem to have been fully appreciated. The earlier writers were concerned with demonstrating the similarity of these plants with the ferns, from which they were supposed to have been derived, and they described them in terms derived from the ferns. But it now seems that in their reproductive structures the pteridosperms were much more comparable with the later gymnosperms and the angiosperms than with the ferns. Pollen and ovules were borne at the tips of fertile branches, and the plants were probably dioecious. There is no trace of hermaphrodite structures, and I am sure that the appearance of bisexual flowers in the Bennettiteales and the flowering plants was a relatively late and not a primitive feature.

The microspore or pollen-bearing organs of the pteridosperms are often described in the text-books as fertile pinnules producing marginal sporangia. This is not an objective description of the pollen-bearing organs produced by the *Lyginopteris* plant, and it certainly cannot be applied to most of the other forms such as *Potoniea* or *Dolerotheca*. We now have some knowledge of about twenty distinct types from the Upper Palaeozoic rocks, and all of them are variants of a radial group of elongated sporangia produced at the tip of the fertile branch. The receptacle bearing the sporangia was usually a disc or cup-like expansion of the fertile axis, with a number of sporangia on its upper side, on its margin, or on its lower side. This change in position, which is sometimes to be seen in a single specimen, was probably due to differences in the rate of expansion or division of the cells on the two sides of the receptacle. Six genera are known from the Lower Carboniferous in which the synangia or sporangia are free from each other, but in the later Carboniferous rocks we find a number of forms in which the sporangia were concrescent, and a large compact structure was produced, in one case with a diameter of 4 cm. Most of these types are only found as flattened compactions in beds of shale, and, since their original form is not clearly seen, there has been some difference of opinion as to what they were like when living. But there is now little doubt about the radial construction of several of the forms, and I think that it is reasonable to describe them as male flowers. For comparison with the angiosperms it is worthy of note that the earlier forms seem to have had a whorl of sporangia on a small receptacle, but in several of the later types the receptacle became a more massive cup-like structure bearing a large number of sporangia and showing a superficial resemblance to the male flowers of the poplars. One very interesting form *Dolerotheca* has recently been described by Schopf from American petrified material, which had a large saucer-shaped receptacle with a very large number of sporangia arranged in rows on its upper side ; the sporangia were in pairs, and between them was a compact tissue of small rounded cells. In some other genera the sporangia were either produced in pairs or had a longitudinal septum of sterile tissue between two loculi. This may perhaps be compared with the structure of the angiosperm anther. Unfortunately few examples of these structures in a petrified condition are known, and some of the examples that have been found require further investigation. One would like to know more about the specimens described in 1922 by Margaret Benson, called by her *Heterotheca* and attributed to *Heterangium*. Dr. D. H. Scott had examined her specimens and entirely disagreed with her description of them, as published in the *Botanical Gazette*. The slides were sent to me for my opinion ; they showed sections through a mass of partly decayed material but did not at all warrant the descriptions that were given, and are now regarded as authentic.

It is usually supposed that in all the pteridosperms the ovules and micro-

sporangia were borne on the leafy fronds, but this is quite uncertain. Very few examples have been found with the reproductive structures attached to fronds though many thousands of fronds must have been collected. It is highly probable that in many of the species the pollen and ovules were produced on fertile branches borne on the main stems, as in the majority of the seed plants. It is of interest to find that the ovules of the *Lyginopteris* plant were produced at the tips of slender branches which bore a series of small microphyllous structures, which can be regarded as bracteoles and differ in form from the normal pinnules of the plant.

The ovules in the group were relatively complex structures constructed on a radial plan, and differing in this respect from the ovules of the Cordaitales. Their structure has recently been well reviewed by Prof. John Walton and I shall therefore say little about the details of the various forms. It seems clear that here the megasporangium was a terminal structure surrounded by a massive integument that seems to have arisen by the coalescence of a whorl of sterile structures formed below the sporangium. In the early forms these structures, each of which had a vascular strand, were not completely fused, but in later forms the series of vascular strands is the only indication of an origin from separate segments. The integuments were complex in structure having hard, stony cells and stout fibrous cells as well as parenchymatous tissue. This type of integument continued to appear in the Mesozoic Bennettitales and Caytoniales, and is seen among the modern Cycads. It is most probable that the plants in these groups were descendants of the pteridosperms, and the development of stony and fibrous tissues in the testa of many angiosperm seeds, together with the vascular strands in the integuments of the seeds in some genera, suggest that these angiosperms also may have sprung from the pteridosperms.

While the integument of the fossil seeds seem to have grown from a whorl of sterile structures below the fertile tip of the ovuliferous branch, many of the forms had a second, somewhat similar whorl of structures, which formed another enclosing envelope. This is generally known as the cupule, although this term is not entirely appropriate. Here again some of the earlier cupules show a whorl of separate segments, in others fusion of these segments took place to give a continuous or a bivalved envelope. In most of the known species the cupules contained only one seed, but in the Lower Carboniferous *Calathospermum* there were a large number of seeds. From a simple biological point of view some of these cupulate structures might be compared with angiosperm carpels which are not completely closed, but we have no reason to suppose that pollination was not typically gymnospermous. Certain seed-like structures have however been found which look as if they had closed cupules, especially the rare type *Nystroemia*, discovered in China by Prof. Halle. It would be interesting to know more about the actual structure of this form.

The pteridosperms did not become extinct in Palaezoic times and it is interesting to observe how their descendants, found in rocks of Mesozoic age, had become changed from the older forms. Do any of the younger types show structural changes leading towards the forms found in the angiosperms? We have very little knowledge of their stem structure. A very considerable number of different leaves have been found which are recognizable as belonging to seed plants by the nature of their cuticles. Some of them were still fern-like, but they were much smaller in size and more condensed. In a number of distinct groups there were simple and entire leaves, while reticulate venation appeared in unrelated families. This is interesting in view of the information we now possess about the development of the venation characteristic of the dicotyledon leaf from a simple reticulum of vascular tissue. The Caytoniales showed reticulate venation in the leaflets of their compound leaves, which usually had four leaflets though sometimes the number was reduced to three,

two or even one. One of the most interesting leaves, long known but only recently investigated, is the Permian and Triassic type from the Southern Hemisphere and India, *Glossopteris*. This, with the closely similar Gangamopteris, was long thought to be a fern, but is now known to be a seed-bearing plant. Its leaves varied in form but were simple and generally lanceolate with reticulate venation, some had a short petiole. A number of different species have been recognized by their outlines, their venation and the structure of their cuticles. Some of these leaves have been found bearing fertile structures on stalks which arose from the midrib of the leaf, as in certain species of *Streptocarpus* among the modern flowering plants.

The reproductive structures in the Mesozoic rocks referable to the pteridosperms or their derivatives show considerable variety of form. In all cases they were produced at the tips of branches which often formed part of a fertile branch system or inflorescence. The majority of these were unisexual, but bisexual flowers occurred in some of the younger members of the Bennettitales, a related group. The inflorescence was often branched in one plane, like a frond, but in other closely similar forms the branching was radial and alternate. The pollen was formed in elongated sporangia or synangia, generally aggregated in radial groups, but in certain forms the receptacle was elongated and the number of sporangia much increased. Another arrangement is seen in the early Cycads where there was a flat sessile structure like that of the modern forms. The peculiar structures of the Bennettitales differed considerably from all other known forms, though they may be linked with the more usual type through some less known Triassic genera. The ovules were generally widely separated, except in the Bennettitales, where they were closely aggregated into conical or spherical masses. In so far as our knowledge goes all these ovules were very similar in structure to those of palaeozoic times, but were much smaller and had a projecting micropyle which caught the pollen by a drop mechanism. It is interesting to note that in a number of forms the ovules had an inverted or pendulous position, suggesting that of the anatropus ovule in many angiosperms.

It is unfortunate that at present we know so little about the structure of the ovules or seeds borne on the fronds of *Glossopteris* and *Gangamopteris*. The material described by Mrs. Plumstead from South Africa is in the form of casts which cannot be interpreted with certainty. In my view they represent terminal aggregations of ovules closely packed together and enclosed in a bivalved cupule. Mrs. Plumstead does not, however, agree with this interpretation.

Entire or bivalved cupules surrounded the ovules in the Corystospermaceae, and almost enclosed them before fertilization. There was a reduced cupule in the Bennettitales, but little or no evidence of a cupule in *Peltaspermum* or *Beania*. The situation in the Caytoniales is very interesting. Here there were a number of ovules, probably arranged in two rows, inside a stout cupular envelope; this was at first open and admitted the winged pollen grains, but afterwards it became completely sealed up. The opening was situated close to the stalk on which the cupule with its ovules was produced, so that it had the inverted form to which I have just referred, and here again we have some evidence that fertilization was effected by a drop mechanism. After fertilization the wall of the cupule seems to have become fleshy, and it would appear from associated coprolites, that these structures were eaten by small animals. The plants of this group, which I discovered more than forty years ago, are thus very interesting, as showing an approach to the angiosperms in their leaves, their anthers and their fruits. But, as I pointed out in 1931, we cannot regard them as ancestors of the flowering plants.

In view of the occurrence of radially constructed flower-like structures in Palaeozoic rocks, one might expect to find evidence of objects more closely resembling angiosperm flowers in the older Mesozoic beds. Such structures do

in fact occur in the Triassic rocks of South Africa, though they are only known from three or four specimens, and the publication of their description has been deferred until further specimens have been sought. They were found some years ago by Dr. Du Toit and Mr. Pyke, and I hope to find additional specimens in the course of the next few months. The specimens already known are very like inflorescences bearing flowers, but the preservation is such that neither pollen-bearing nor ovule-bearing structures can be identified in them with certainty. In one form, which I am calling Pykea, the flower-like structures seem to have had two whorls of free perianth segments, possibly surrounding some fruits or seeds. In another different form the perianth segments were more delicate and were produced on a small disc-like receptacle with some compressed plant material within them. Bracts and bracteoles occurred on the branches of the inflorescence. Whatever may prove to be the nature of such plant remains they afford another instance of the occurrence in mesozoic times of structures resembling those of some flowering plants. They, like *Williamsoniella* and other members of the Bennettitales, seem to show that the perianth members should not be regarded as modified foliage leaves which have been reduced in size and altered in form. More probably they are organs produced *de novo* by morphogenic processes in parts where there were no similar structures before. In earlier times a whorl of sterile structures grew up around the megasporangium, then a second whorl formed the cupules, now a third whorl appeared surrounding the terminal groups of ovules or flowers.

Taking the fossil record as a whole, one may say that there is no certain evidence of the presence of angiospermic flowering plants on the earth before the Cretaceous period. There is, however, abundant proof of the existence from much earlier times of a large and widespread group of woody seed-plants, which approach the dicotyledons in the stem structure, in the form of their leaves, and in their inflorescences. Some of them produced their pollen in structures comparable with antlers ; their seeds show certain resemblances to angiosperm seeds. The presence of an envelope around the ovules was an early feature, and in one group this envelope was almost closed. While we have as yet no knowledge of when and where the final details of angiosperm structure were achieved, the great gap which at one time seemed to separate the modern flowering plants from all other known vegetable types has been considerably narrowed.

This position has been reached partly by the discovery of the remains of ancient plants whose existence was unsuspected fifty years ago, and partly by the realization that the old concept of the *Urform* in plants had no materialistic significance. Nowhere in the fossil record do we find forms really comparable with the type which has been imagined as the primitive flowering plant. Flowers have never been really made up of an aggregate of fertile and sterile leaves in the objective sense. There is no trace of entire fertile leaves bearing marginal ovules, which might have evolved into carpels. The historical evidence suggests that floral structures evolved in a totally different way, a way which is consistent with what we know of the physiology of flower production. The geological record suggests to me that the flowering plants have been evolving very slowly since the Palaeozoic epoch. The large number of genera which appeared in the Cretaceous period must have had a long previous history. Their apparently sudden appearance was more probably due to ecological factors than to any kind of explosive evolution. We know that major climatic changes occurred in the past and that these were followed by revolutionary changes in the vegetation of the regions concerned. The sudden appearance of the flowering plants may well have been due to changes of both a climatic and a biological character in the environmental conditions.

In concluding my remarks I must remind you that the study of fossil plants

by the technical methods now available is of comparatively recent growth, and that the number of workers engaged in it has been small in comparison with those studying other branches of botany. Considerable thicknesses of rock over a wide area of the earth remain to be investigated, and there can be no doubt that much remains to be discovered. But the work of the past century has brought us so much evidence of evolution that the problem of the origin of the flowering plants, though not yet solved, is perhaps less baffling than it appeared to Charles Darwin, when he called it an abominable mystery.

I think that we have reached the stage when the flowering plants now living should be re-examined in the light of the historical evidence which I have tried to summarize. We should consider their possible interrelationships from a new standpoint, in place of the idealistic outlook developed from the scholasticism of Linnaeus and the purely philosophical approach of Goethe. This may bring us a fuller understanding of the world of living things among which we live.

THE DICK HERBARIUM: ADDITIONAL NOTE

By Sir Gavin de Beer, F.R.S., F.S.A., F.L.S.

[Received 24 May 1957.]

In a paper on the Dick Herbarium (*J. Linn. Soc. Lond. Bot.* **55**, 1955, p. 225), I referred to the acquisition of this herbarium by Sir Joseph Banks in 1775. At the time when he bought it, he did not know the name of the collector, and it was Jonas Dryander who later supplied the information : " It was Dick."

Among the manuscripts preserved at the Royal Botanic Gardens, Kew, is a letter from Jean-André De Luc, F.R.S. (1727–1817) dated 10 March 1779 bearing on this subject. The person to whom it was addressed is not specified, and as it does not appear from internal evidence to have been Banks himself, it was probably Daniel Solander, Banks's Secretary.

By the kindness of Dr. George Taylor, Director of the Royal Botanic Gardens, Kew, it is transcribed below.

Kew. B.C. 1.81.

Sir

I have traced up Mr. Dick's Herbarium from his death. It was sold by the widow to Mr Engel of Berne who had the commission from M. Gaussen of Geneva who has send it to J. Banks Esq^{re} in London. So you know now where it is. I hope my success in this little commission will encourage you to honour me with all those that you might have to execute in Switzerland.

I am with the greatest regard
Your most obedient humble servant
J. A. DeLuc.

Pimlico ye 10 March 1779.

It remains to add that De Luc who was born in Geneva was at the time Reader to Queen Charlotte, and was the obvious person to whom to apply in England for information about scientific matters in Switzerland. Samuel Engel (1702–84) was a cousin of Albrecht von Haller whose Mother was Anna Maria Engel. As Dick had been tutor to Haller's children it was natural that Engel should interest himself in the welfare of Dick's widow. Paul Gaussen (1720–1806) was a keen amateur botanist and horticulturist who befriended Thomas Blaikie in 1775. As Blaikie had been sent to Switzerland by Dr. Pitcairn it was natural that Gaussen (who must therefore have been " a correspondent in Switzerland ") should suggest to Engel that he should offer Dick's herbarium to Pitcairn who passed on the offer to Banks.

LOGIC AND MEMORY IN LINNAEUS'S SYSTEM OF TAXONOMY.

By A. J. Cain
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[Received 25 April 1957.]

Contents.

	Page
Introduction	144
Logic	145
(i) Genus and Differentia	145
(ii) Taxonomy of Unanalysed Entities	146
(iii) Definition	147
(iv) Division	149
(v) Gaps between Groups	152
(vi) The Idea of a Natural System	154
Memory	
(i) Requirement and Consequences	156
(ii) Natural Genera	157
(iii) Monotypic Genera	158
(iv) Distinctness of Genera	160
Bases of the Linnaean System	161
Summary	162
Acknowledgments	162
References	162

Introduction.

Taxonomists have been consulting Linnaeus's books ever since he wrote them, in order to improve his and their own arrangements, definitions, or nomenclature of particular sorts and groups of living things, both plants and animals. Svenson (1945) has reminded us of Linnaeus's actual methods of description and nomenclature, and has discussed briefly his notions of the variety, species and genus, and the natural system. Ramsbottom (1938) has examined in detail the changes in his notion of the species. I myself (1956) have discussed the genus in Linnaean and subsequent taxonomy. There is also a highly significant remark by Uggla (in Schmidt, 1952) on Linnaeus's use of logic. Apart from these, few have commented at all on the theoretical considerations that influenced him.

They should be examined for two reasons. In the first place there is no better method for scientists of one period to bring to light their own unconscious, or at least undiscussed, presuppositions (which may insidiously undermine all their work) than to study their own subject in a different period. And secondly, when the writings of an earlier author have apparently been taken as the basis of subsequent work, constant scrutiny is necessary to prevent his presuppositions becoming fossilized, so to speak, in the subject and producing unnoticed inconsistencies when modifications have been made as a result of subsequent work.

In the course of a comparison between Linnaeus's principles and those appropriate to evolutionary taxonomy, it became obvious that two of the most important features of his system had hardly been commented on. These are, his use of the general principles of all classification laid down by Aristotle in his *Logic*, and his insistence that all botanists must know and remember all the genera. The peculiarities of Linnaeus's system are in great part consequences of these.

This paper gives a brief survey of their effects, as a preliminary to a detailed study of Linnaeus's own theory of taxonomy, not as a revision of his arrangement of any particular group of organisms. Quotations are usually given in English for convenience ; the translations are my own, as few suitable ones are available. The elegant translation of the *Critica Botanica* by Hort (1938) has unfortunately sacrificed terminological accuracy to literary polish and is consequently unsatisfactory in its rendering of words which to Linnaeus were technical terms and therefore not to be replaced for aesthetic reasons by any of a number of vague synonyms.

Logic.

(i) *Genus and Differentia.*

In the present state of Western education it is easy for biologists to forget that every well-educated man in and before Linnaeus's time might have been given some instruction in the principles of classification in general, as laid down by Aristotle. This he would receive in the study of *Logic* ; and in consequence some terms such as Definition, Genus, Differentia and Species would have for him as general an application and significance as is possessed to-day, for most biologists, only by Definition or Difference, terms obviously not confined to biological taxonomy. Useful introductions to this system of Logic and its corresponding philosophy are given by Maritain (1946*a*, 1946*b*) and an important full discussion by Joseph (1916).

A brief summary of the Aristotelian position as it concerns this paper is as follows. If B is predicable of A, it stands to A in one of five relationships ; it may be a Definition, a Genus, a Differentia, a Property, or an Accident. The *Definition* of a subject is the statement of what that subject must be in order to be just that and not something else, the statement of its *essence*. The essence cannot be changed and the subject remain the same. The essence is that which mediates its actual existence (Maritain, 1946*a*). The *Genus* is that part of the definition (and essence) of a subject which is predicable also of other subjects. For example, in the famous definition of Man as a reasoning animal (*animal rationale*) the genus is animal, which can be predicated not only of man but of other living beings (namely, non-rational animals) as well. The *Differentia* is that part of the definition which is not predicable of other species in that genus, and therefore expresses the difference between a particular species and all others in the genus. A *Property* is an attribute of any subject which is common and peculiar to it, and follows from its essence as a consequence ; it is therefore not included in the definition. An *Accident* is any other attribute of a subject, which has no necessary connection with its essence, and may or may not be present in any given individual of it. For example, the colour of a jug has no necessary connection with its " jugginess " and can vary without having any effect on it.

According to Aristotelian logic, the genus should not be regarded merely as a collection of species. The genus and the differentia taken together are the definition of the species, the statement of its essence ; " the genus is the general type or plan, the differentia the ' specific ' mode in which that is realized or developed . . . " (Joseph, 1916, p. 83). Consequently, " Individuals are not included in one genus because agreeing in certain attributes, and then in one species within the genus because agreeing in certain other attributes that have no connection with the first ; as you might include in one island all men who had red hair, and then rail off separately within it those of them who had wooden legs ; *wooden-legged* could not be a differentia of the genus *red-haired* ; it must be some modification of red-hairedness itself, and not of the men having it, which could serve as a differentia to that genus. It is therefore a phrase that may mislead, to say that the differentia *added* to the genus makes the

species, or makes up the definition. For adding suggests the arbitrary juxtaposition of independent units ; but the differentia is not extraneously attached to the genus ; it is a particular mode in which the genus may exist. And hence, when we distinguish the various species of one genus, in what is called a logical division, assigning to every species the differentia that marks it off from the rest, our several differentiae must be themselves homogeneous, variations, as it were, upon one theme . . . The principle that the differentiae must be thus cognate is technically expressed by saying that there must be one *fundamentum divisionis* . . . " In the genus triangle for example, if one species is isosceles, the others will be equilateral and scalene, the *fundamentum divisionis* being here the proportions of the sides ; but to have one species isosceles and another right-angled means that two *fundamenta* are being used simultaneously, and this is illogical.

Obviously, to classify in this way is most important, if it can be done, since by exhibiting the essence one is showing what each species really is, and what are the fundamental differences between it and the others in that genus.

(ii) *Taxonomy of Unanalysed Entities.*

But in such a classification the essence of the species must be determined before a definition, by genus and differentia, can be produced. Now it is true that where *a priori* knowledge is concerned, we can determine what is the essence of any subject necessarily ; that of plane triangularity, for example is " a plane figure bounded by three straight lines ". What follows necessarily from such a definition will be a property of the subject, what does not (e.g. the colour of the lines actually used to bound one such figure) will be accidental. The ideal classification described above can therefore be put into practice. Mathematics, and especially geometry, studied by both Plato and Aristotle, is the most obvious example of a subject-matter suitable for classification by genus and differentia.

But when we cannot, or at least do not, see the necessary connections between the essence and the properties, and do not know what is a property and what an accident, and indeed can approach no nearer to a definition than a mere statement of what we intend a particular word shall mean, such a classification becomes impossible. We can only proceed empirically, simply finding out what subjects exist and what are their attributes, not deducing them from known principles and axioms. Where logical division is possible, we can have a *taxonomy of analysed entities* ; where not, only a *taxonomy of unanalysed entities* is possible, and the best example of it is indeed biological taxonomy.

This difficulty with regard to the subject-matter of biology and other natural sciences has, of course, been recognized by logicians for centuries. Maritain (1946*a*) in his introduction to Aristotelian and Thomistic philosophy puts it thus (p. 154). " It is important to bear in mind that the experimental sciences are very far from being able to know perfectly the essence of the things which they study. They are, in fact, unable to attain a truly distinct notion of their essences, and never possess more than a confused or purely descriptive notion of them. They know them, so to speak, after the fashion of a blind man by means of indirect signs." Joseph (1916) remarks that " the problem of distinguishing between essence and property in regard to organic kinds may be declared insoluble. If species were fixed : if there were in each a certain nucleus of characters, that must belong to the members of any species either not at all or all in all : if it were only upon condition of exhibiting at least such a specific nucleus of characters that the functions of life could go on in the individual at all ; then this nucleus would form the essence of the kind. But such is not the case. . . . There may be deviation from the type, to a greater or lesser

degree, in endless directions ; and we cannot fix by any hard-and-fast rule the amount of deviation consistent with being of the species, nor can we enumerate all the points, of function or structure, that in reality enter into the determination of a thing's kind. Hence for definition, such as we have it in geometry, we must substitute classification ; and for the demonstration of properties, the discovery of laws. A classification attempts to establish types ; it selects some particular characteristics as determining the type of any species ; these characteristics should be (*a*) of the same general kind for each type within one genus, or . . . variations upon the same theme, in order to exhibit the mutual relations of agreement and divergence among the various types : (*b*) important, or, as one might say, pervasive : that is, they should connect themselves in as many ways as possible with the other characters of the species. It will be the description of the type, drawn up on such principles as these, that will serve for definition".

The relevance of these quotations from logicians for the whole history of biological taxonomy from Aristotle to the present day can hardly be overestimated. They epitomize the most important change in taxonomic theory that has occurred, namely the gradual abandoning of attempts to set up classifications on *a priori* principles agreeable to the rules of logic and some particular theory, and the partial substitution of an empirical attitude. This substitution was not complete when the theory of evolution arrived to provide a new theoretical approach to the problem of classifying organisms, the full implications of which have still not been completely thought out. Moreover, in the quotation from Joseph, we see the logically trained mind finding a practical solution to the problem by setting up just such a system of types as was in fact evolved by taxonomists, and doing so for exactly those reasons, as I believe, that influenced them, namely that this was the best approach to a logical division that could be made. The principles of logic were still their guide and pattern. It is not surprising, therefore, that Linnaeus should declare the arrangement (*Dispositio*) of plants to be theoretical, which institutes the Classes, Orders and Genera, or practical, which institutes the species and varieties and can be carried on without the knowledge of any System (*Philosophia Botanica*, Aphorism 152). Theoretical arrangement for Linnaeus is that to be carried on according to principles, practical that which can be only empirical.

(iii) *Definition.*

As Hopwood has reminded us (1950), certain rules can be given for defining anything, to avoid tautology or irrelevance. Those he gives are as follows.

1. The definiens [defining expression] must be the exact equivalent of the definiendum [that which is to be defined] ; it must be neither wider nor narrower in its scope.

2. The definiens must not include any expression which is contained in the definiendum, or which could be defined in terms of the definiendum. (Otherwise, to that extent the definition is circular.)

3. The definiens must be expressed in the clearest possible terms.

4. The definiens must always be positive unless the definiendum itself is negative.

These rules are purely formal (except perhaps No. 3, which is primarily aesthetic or economical) and have no foundation in any particular philosophical theory. It is of interest to compare them with those given by Joseph, which are more closely Aristotelian and therefore more like those which Linnaeus would have been taught to observe. In these, the above four are given, in different words, but there are two others which are placed first, namely :—

1. A definition must give the essence of that which is to be defined [and

where this is impossible, one must just do the best one can, along the lines suggested in the quotation given on p. 147].

2. A definition must be *per genus et differentiam* (*sive differentias*). The reason is that this indicates both the general kind of the subject, and the attributes which qualify it in particular.

The addition of these two rules firmly attaches the theory of definitions to Aristotelian logic in particular. Linnaeus's own ideas on definition were clearly based on Aristotle's as far as possible. The *Generic Character* (not character in the modern taxonomic sense, for which he always used *nota*, a note, characteristic or mark) is the same as a definition of the genus. ("Character genericus idem est ac *Definitio generis*" *Phil. Bot.*, Aphorism 186). The *Essential Character* of a genus is that which gives some characteristic peculiar to it, if there is one such, which will instantly serve to distinguish it from all others in the same natural order. (The *Natural Character*, which is the best, contains all the generic characteristics of each genus and is the most difficult to draw up; the *Factitious Character* is one that distinguishes a genus from all others in an artificial order and is used only as a succedaneum (*Phil. Bot.*, 190) until the natural classification can be discerned.) The true specific name is a *Differentia essentialis* (*Phil. Bot.*, 257) distinguishing that species from all others in the same genus—and Linnaeus insisted that all genera are natural. Specific names taken from hypotheses—i.e. those based on artificial classifications made according to preconceived rules—are false (*Phil. Bot.*, 258). The *Character naturalis* of a species is a description; the *Character essentialis* is a Differentia (*Phil. Bot.*, 258).

From these statements, it can be seen that the essential character, i.e. one that states the essence, and the differentia are respectively that which defines uniquely the general kind (genus) and that which states the peculiarities that characterize one particular species (differentia of the species within the genus). This is pure Logical Division. But, as already shown, such definition is appropriate only to a taxonomy of analysed entities; here we have no such thing, and it is understandable, therefore, that Linnaeus found himself unable, because of the empirical facts, to prescribe any set principles on which species could be differentiated, or to accept the first division into woody and herbaceous plants made by Cesalpino (1583) on first principles. Yet he maintained the necessity of basing the theoretical part of classification on the fructification, which is the next division on Cesalpino's principles.

It is easy to see how the emphasis of the logical aspect of such a theoretical classification, with the obvious reminder that only individuals exist in Nature, not genera as such, will very readily suggest that the genus in the logical sense is an abstraction, a general idea, existing only as far as it is realized with modification in the individuals of particular species. The step from this to its being an Idea in the mind of the Creator is reasonable; the species of a genus are then variations on a supernatural theme. From this point of view Fries (1835, p. xvi) was right in saying that the classification expressed "*quoddam supranaturale*". Linnaeus, too, was quite right on his own principles in insisting that *because* the stamens, pistil, etc., subserve the extremely important function of genuine sexual reproduction, the classification must be based upon them; in this he was following the rules of logical division and the practice of Cesalpino by trying to get at the essence. Sachs's criticism (1875), perfectly right in practice, that they would be just as useful if their functions were unknown or they had none, reveals a considerable misunderstanding of Linnaeus's point of view. Whether in the then state of knowledge, it is reasonable to expect that Linnaeus ought to have perceived the impossibility of any taxonomy of analysed entities, and have gone straight over to a purely empirical classification, as Sachs implies, I do not know. Sachs (1906, pp. 41,

81, 92) makes the special point that Linnaeus was the first to appreciate the difference between artificial and natural classifications, and takes that to mean the difference between a classification founded on predetermined principles and one according to natural affinity ; consequently, he blamed him (1906, pp. 101–102) for not working more assiduously at the natural system. I think, however, that what Linnaeus meant by the natural system was not quite what Sachs meant (see p. 154), and in consequence have put the word *natural* into quotation-marks when the Linnaean meaning is intended. De Candolle (1813) also stated that Linnaeus was the first to separate natural and artificial methods, but his usage of the word "natural" is much more like that of Linnaeus (Cain, in preparation).

What Linnaeus did find, at least in practice, was the ease of transition from the purely logical attitude to the empirical in which the genus is indeed a larger group containing its species as smaller constituent groups. And since one could not know what sort of species with what peculiarities would turn up next, the application with any consistency of the principle that in every genus there must be only one *fundamentum divisionis* very rapidly became impossible. It is not surprising that he described the *Dispositio* of species and varieties as practical and not theoretical. By experience it was known that they could be determined only by going and seeing. Once discovered, they could be arranged according to pre-determined principles, of which important ones for him were that groups must be based on the fructification, and that in any sort of classification the genus and species must be "natural", and the sooner the other groups could be made so, the better.

Linnaeus was never faced with the problem of defining separate and distinct sorts in either a time-series of fossils or a widespread species showing continuous geographical variation. Definition in the logical sense of separate entities, as remarked above, is not possible in a taxonomy of unanalysed entities, and this was a serious problem for him ; but the possibility that sorts of organisms might intergrade *smoothly* in time or from one country to another seems not to have arisen. Where continuous variation between otherwise distinct sorts occurs, the *universal* application of the definition of discrete groups breaks down. Biologists have known this for many years but only recently has it become an urgent practical problem. The rules of definition given by Hopwood are free from any reference to essence, genus and differentia ; but they still presuppose that there are definienda with ascertainable limits. Some of the greatest difficulties in the species-concept at the present day arise because that presupposition is not obviously justified (Cain, 1953, 1956 ; Mayr, 1942 ; Simpson, 1951).

(iv) *Division.*

The process of taking a particular genus and distinguishing the species within it is called Logical Division. And "the better our division of the genus into its species, the larger will be the number of general propositions that can be made about its species or parts" (Joseph, 1916, p. 115). The utility of good division is therefore obvious, and it is not surprising that systematists wished to follow it as closely as possible. The close connection between division and definition is also obvious. Joseph uses classification as the opposite of division ; in division the general kind is broken up into specific modes, in classification the species are brought together under their proper genera. If division (or classification) is carried through several stages, the technical terms for the stages are *genus summum* for the main kind to be divided, *genera subalterna* for the intermediate kinds into which it is divided and for their divisions similarly, until one reaches the *species infimae* with which the division stops. Linnaeus specially quotes this hierarchy (*Phil. Bot.* 155 ; *Syst. Nat.*, 10th Ed.,

p. 7, and partially in *Crit. Bot.*, 251) in the form Genus summum, Genus intermedium, Genus proximum, Species, Individuum, as an exact parallel with Class, Order, Genus, Species, Variety. (In fact, it is not strictly parallel since logical division, dealing necessarily only with universals, cannot proceed to the individual as such and the Variety is still a universal.) The same hierarchy was used explicitly by Ray and others of Linnaeus's predecessors as their arrangement of ranks.

The rules given by Joseph, by which division must proceed in Aristotelian logic, can be stated as follows.

1. A division must be exhaustive (otherwise something will be omitted).
2. The constituent species of the genus must exclude each other (otherwise there will be an incomplete separation and therefore faulty definition of the species).
3. A division must proceed at every stage, and so far as possible through all its stages, upon one principle, or fundamentum divisionis.

Only if a single fundamentum is used in each group will the species actually exclude each other. A division of the genus *Metazoa* into Diploblastica, Triploblastica and Parasites is clearly illogical and conducive only to confusion ; it is proceeding on more than one fundamentum, and is called a cross-division, since the division by one fundamentum cuts across that by another. However, genera may be divided on the different *combinations* of the same set of characters without this error being committed, and distinguished well (logically) if the possible combinations can all be stated.

This does not mean, of course, that the fundamentum must not change throughout a hierarchy. There is no objection to dividing the genus Animal into Unicellulars and Multicellulars and then dividing the genus subalternum Multicellulars into Coelomata and Acoelomata. But the more changes of the fundamentum, the more differentiae must obviously be entered in the definition of any one species infima. Consequently it is better to proceed as far as possible on a single fundamentum. It makes for conciseness and a more direct appreciation of the nature of each species and its relations with others. As is shown later (p. 157), conciseness and clarity of idea presented by a name were specially valued by Linnaeus, and for him the specific Differentia was a name.

These rules of division have had an enormous influence on our classification of organisms. The logical necessity of defining clear-cut discrete groups was a practical necessity in Linnaeus's day (and still is for keys) but has almost no justification theoretically in evolutionary taxonomy even though it retains its importance in badly known groups (Mayr, 1942 ; Simpson, 1951 ; Cain, 1953, 1956). How often its prestige has driven the taxonomist to " define " groups which cannot in fact be defined although they are clearly natural (Cain, 1954), or worse, to mutilate his natural groups until each is definable, a study of the whole taxonomic literature would show, and the result would be depressing. One thing is quite obvious, that the overworked taxonomist, required to get out such a classification, will inevitably use the most striking characters as basis for his " definitions " because *they will be the most easily described in words*, and they may then assume a wholly disproportionate importance in his classification. The most striking and easy division will be made first, and by an insidious change of emphasis will be taken to be, first, most fundamental logically, and then in the present age of taxonomy, most fundamental in an evolutionary sense. Often it can be seen that by this last is meant that the particular divergence in question was a great step forward (on whatever definition of evolutionary progress the particular taxonomist fancies) or was very hard to achieve, or took place very long ago, or could not be expected to have happened more than once, or all of these. This is usually the real basis of the assumption that greater overall differences between related forms indicate

a more remote common ancestry, and lesser ones a more recent, as though the evolution of morphological (or any other sort of) diversity goes on at the same rate in all lines of every group. It may be argued that where the fossil history is unknown, this assumption is all we have to go on ; the reply is that when one has nothing to go on, it is better not to go, and not to pretend that a classification is phyletic when it is not.

Fortunately, there are correctives which can be applied in practice. Even striking characters must be disregarded if found to vary from one individual to another, or from species to species in a group which on all other characters seems to be natural and not very heterogeneous. Under such circumstances, the taxonomic importance of a character is determined by its covariation with all other characters within a group (Cain 1953, p. 25).

Linnaeus uses division in the logical sense given above. For example, in *Critica Botanica*, Aphorism 285, which states that the generic must precede the specific name, he says " Whatever makes the first division should be given first, consequently the generic is stated before the specific name : before I distinguish something I need to know what is to be distinguished, and so I shall give the genus which is divided into parts by the differentia, before I touch the species ". This corresponds exactly with Joseph's second rule of definition (p. 148) and illustrates the close connection between division and definition. What Hort translates as " the classification of the Ancients " is *Veterum divisiones* (*Crit. Bot.*, 246), and a similar use of the term division occurs many times. For example (*Phil. Bot.*, 152) " Arrangement teaches the Divisions or Conjunctions of plants ". Again, the parallel given above between the hierarchy of logical division and of the taxonomic ranks, and the statement (*Phil. Bot.*, 204) that the Order is the (logical) genus of (taxonomic) Genera, but the Class is that of Orders, and the description of Orders as " Classes subalternae " (*Genera Plantarum*, 1764, p. 5), are entirely appropriate to logical division.

Sachs (1875), who has stressed Linnaeus's indebtedness to Cesalpino, says that Cesalpino's ascription of great importance in botanical taxonomy (after the division into woody and non-woody plants) to the fructification is because it subserves the second most important function of plants, namely to reproduce themselves. (The first, connected with presence or absence of woody tissue, is to feed.) As the 1906 translation of Sachs gives it, " Though these parts [the fructification] are only found in the more perfect forms, yet the subdivisions (' posteriora genera ') must be derived in both trees and herbs from likeness and unlikeness in the fructification. And thus Cesalpino was led, not by induction but by the deductive path of pure Aristotelian philosophy, to the conclusion that the principles of a natural classification are to be drawn from the organs of fructification ; for which conclusion Linnaeus declared him to be the first of systematists . . . " (What Linnaeus actually called him was *primus verus Systematicus*, the first true systematist (*Phil. Bot.*, para. 54) which is not quite the same thing. The original German (1875, p. 57) gives " ein Satz um deswillen Linné den Caesalpin als den ersten Systematiker seierte ", which is a better rendering of Linnaeus's remark.)

Whatever the theoretical reason given, there is a good practical reason for paying considerable attention to the fructification ; it is usually morphologically the most complex organ-system of the plant and provides a large number of characters for study and comparison. Moreover, some at least of its constituents are usually reduplicated a definite number of times (e.g. the five sepals and petals of the common field buttercup, the two long and two short stamens of many labiates etc.). Number is a particularly good attribute for use in a division which is to be as logical as possible. It is easily ascertained, expressed, and understood, and clear-cut if only the integers are needed. Linnaeus analyses

the variation in structure of the fructification into Number, Figure (shape), Proportion, and Situation (*Phil. Bot.*, 92–97 ; *Genera Plantarum*, title-page) in that order. He found it suitable, therefore, for a logical division. At the same time, when the flowers and fruit of two species, in all their peculiarities and complexities of structure, are closely similar, it seems reasonable to believe that the two are closely related, even though their leaves or root or mode of growth may differ. (He himself says (*Phil. Bot.*, 163) that the fructification opens the highroad to the natural method.) Exactly the same procedure is used in would-be evolutionary taxonomy of any group in which the fossil evidence is insufficient ; the guess is made that two forms agreeing in such a large character-complex are most unlikely to have evolved it independently and must therefore be regarded as closely related phyletically.

It would seem, then, that the real justification for Linnaeus's choice of the fructification is the empirical one. But if so it need not be derived from any theoretical considerations such as Cesalpino professed. That Linnaeus did adopt them is suggested by the fact that he declares the fructification to be the true foundation (*fundamentum*) of all Method, without qualification (*Phil. Bot.*, 26), and is therefore using it as a single *fundamentum divisionis* in strict accordance with the third rule of division (p. 150), so he must have regarded it as of prime importance for understanding the essences of plants. However, he had already found it necessary to abandon the primary distinction between woody and non-woody plants since it so obviously separated extremely closely related forms. Svenson (1945) has shown in his discussion of the genus, how soon after Linnaeus the mere weight of empirical evidence caused a similar rejection of the doctrine that all genera were "natural" and distinct. Certainly, at the present day, even the best-known genera can be called natural only in a very restricted sense (Cain, 1956).

Linnaeus was indeed remarkably successful in his application of the principles of logical division to the production of an artificial system—in other words, a key ; and one need only think of the characteristics of a good key to realize that these principles are very suitable for its production. The characters chosen from the fructification were clearly marked, readily appreciated, easily described in words, and usually determinable on herbarium specimens. One tends to forget that for Linnaeus the Class and Order, being indeed only names for genera subalterna at different stages of division, were as applicable to an artificial as to a "natural classification". Nowadays, the ranks of the taxonomic hierarchy are not used (except incidentally) in a key. Linnaeus's own remarks on the Class and Order are that the Class is a large group of genera which agree in important characters, and so that there should not be too many things in one group to be easily distinguished, the Class is subdivided into Orders each of which will contain a manageably small number of Genera ; since it is easy to distinguish ten things from each other, very hard if there are a hundred (*Phil. Bot.*, 160, 161). The Class is therefore less "natural" than the Genus, and the Order less "natural" than the Class (*Phil. Bot.*, 205). This statement must refer to at least partially artificial systems. Nowadays we hope that all the groups in all the ranks of the classification are equally natural, and Linnaeus would have agreed heartily that a natural system in some sense is indeed what one should aim at.

(v) *Gaps between Groups.*

As the result of his use of Logical Division, Linnaeus's groups had to be clear-cut, divided as far as possible upon one fundamentum divisionis, exhaustive, and exclusive. That this was indeed his attitude even to "natural" groups is clearly seen from his treatment of genera and species, which he

expressly declared to be "natural". He insists that one must have clear and separate ideas, genera and names (*Crit. Bot.*, 225; *Species Plantarum*, introduction), that there can be no such thing as an intermediate between genera (*Crit. Bot.*, 224), and that in the definition of genera and species only those characters (in the modern sense) which are truly constant and peculiar can be used (*Crit. Bot.*, 256), which implies that such characters exist for all genera and species.

When the genus is divided, then, the division must be exhaustive. All plane triangles are equilateral, isosceles or scalene in respect of the proportions of their sides, and these terms are so defined that all plane triangles are included in them. But scalene contains triangles differing widely in the proportions of their sides, while equilateral contains only one member. There are in fact two infinities of possible triangles in the species scalene and one in isosceles. An actual continuum of variations is therefore broken up into species of very unequal content. There is, however, no gap between the species, which are contiguous. The only vacant species in this division must be a species of all plane triangles which are neither equilateral, isosceles nor scalene—i.e. a species which cannot be exemplified because its definition is a contradiction in terms.

Now we can see that if flowers have stamens and these are discrete entities, they must have either 1 or 2 or 3 or 4 . . . and so on. It does not follow, however, that actual flowers exemplifying all these classes can be found; in fact Linnaeus had to omit from his sexual system the class of flowers with 11 stamens (*Phil. Bot.*, 68) because it was not known to be exemplified. In such a classification absentees can be detected when all existing forms have been discovered, but their absence can only be noted as an empirical fact. Given the definitions of plane triangle, scalene etc., one can see that no other species of triangles are possible; but given the definitions of flower, stamen, and positive integers, one can see no reason why flowers with any number should or should not exist. The absence of a class does not mean that its definition is internally contradictory, and it tells us nothing about the nature of the gaps between exemplified classes; these may be either parts of a continuum, as in the example of triangles given above, or discrete entities, as are for example the species of the genus Regular Polygon as differentiated by the number of sides.

In the current system of taxonomy the meaning of some gaps, at least, is quite definite. If one species is placed by itself in a monotypic genus and that in a monotypic family, while adjacent families contain many genera with many species, this is interpreted as meaning that the overall differences between the first-named species and its nearest relatives are far greater than those between other closely related species or even genera within the group of all species under consideration, and about as great as those between families. No precise account of what is meant by overall difference or resemblance (i.e. affinity) has yet been produced, and this is one of the principal necessities in taxonomic theory (Cain & Harrison, in preparation). What is clear, however, is that rank in the taxonomic hierarchy is being used as a rough measure of the homogeneity of a particular group, and of the difference between it and the most closely related of known groups, on some sort of subjective scale of similarity. The procedure could easily be extended to other subjects—for example, in the genus Regular Polygon, the overall morphological difference between the members of the genus clearly decreases as the number of sides increases. There is more difference morphologically between an equilateral triangle and a square than between a twenty-sided and a twenty-one-sided regular polygon, and as n rises towards infinity the resemblance to a circle becomes ever more perfect. But in strict Logical Division, such a criterion is clearly useless; it is merely

an overall estimate based on the properties (if the essence is known, or merely on properties and other attributes indiscriminately if it is not) and as such does not give the essence, from which all the properties would follow. To use it would be like working from a description of all the reactions which a given chemical element can take part in instead of determining its atomic number and other characters, when classifying chemical elements. In fact, it would mean being content with plain description with no attempt at analysis, or nowadays with no attempt at experimental analysis where this is in fact possible; one must constantly remember that for most people at the time of Linnaeus, Logical Division did mean the attempt to find out the real *nature* of things instead of being content with mere superficial appearances; their mistake was to apply it to all subjects instead of restricting it to *a priori* knowledge, and considering the triumphs of mathematics as applied to musical harmony by the Greeks and to mechanics by Galileo, Newton and others, the belief that principles discoverable purely by the use of reason could be found throughout Nature was not unreasonable, at the time.

As far as Linnaeus retained the principles of Logical Division, then, he was in *theory* committing himself to the view that the principles upon which plants were constructed were known, the number and peculiarities of all genera subalterna could be ascertained, and the properties of forms not yet discovered could be prophesied. In practice, of course, no such view could be taken. The most that could be said was that in a system as nearly logical as possible, the place of a species could be determined at once from its own attributes—for example, a species with eleven stamens in order to maintain the symmetry of the system must be put into a different Class from one with ten, when it has been decided beforehand to make the division into classes on the stamens. This makes for efficient identification. But when he tried to work out a "natural" system using overall affinity within the fructification as his basis, it is not surprising that he had the greatest difficulty in defining the "natural" groups by clear-cut characters (in his sense). What we see principally in Linnaeus's system is the conflict between the attempt to base a "natural" system on an analysis of plants by hard thinking according to the best rules available, in other words to create a taxonomy of analysed entities, and the attempt to do so by overall affinities. The bases are different fundamentally, and although the resulting arrangements may coincide to a large extent, it cannot be expected that they should always do so.

(vi) *The Idea of a Natural System.*

The use of the concept *natural* by Linnaeus, therefore, merits further consideration. What in fact did he mean by a "natural" system? It is obviously one that follows Nature. Nature to us nowadays means the world we find and do not make—the opposite of natural is artificial. A devotion to a natural system could mean to us, and often does, an attitude of the purest empiricism. It could hardly do so to Linnaeus. Hawkins (1946), speaking of the philosopher John Scotus Erigena's ideas on Nature, says "Nature here has no narrower signification than reality, but reality, for Erigena, is indeed a nature in the Aristotelian sense, a principle of becoming . . ." In Aristotelian and Thomistic philosophy the word is a technical term of considerable subtlety. Maritain (1946*a*) says "The primary intelligible being of a thing is called *essence* (*essentia*) because since the intellect is modelled on being, what a thing primarily is for the intellect must be that which is of primary importance in it from the standpoint of being itself; in fact . . . it is by and in its *essence* that a thing possesses being or *existence* (*esse*). It is called *quiddity* (*quidditas*) because it is that which the definition expresses and declares, which in turn

answers the question *quid est hoc ? What is this ?* It is called *nature* (*natura*) because it is the first principle of the operations for the performance of which the thing has come into being (*nata*) " and he quotes in support St. Thomas Aquinas (1254) " *Entitas vero rei considerata in ordine ad esse, dicitur* essentia ; *in ordine ad operationem dicitur* natura ". (The being of a thing considered in the order of existence is called essence, in the order of operation it is called nature.)

To appreciate the full subtlety of these remarks and the role of the concepts expressed in them in Aristotelian and Thomistic philosophy a close study of the latter is advisable. Maritain (1946*a*) will serve as a useful introduction, warning us against too simple-minded an interpretation. The relations between the nature and the essence of a subject are not simple—for example, only in the case of pure spirits is the concept of complete essence identical with that of individual nature (p. 158, fn.). But he says (p. 162) " The term *nature* . . . is used in reference to the operations which anything is adapted to perform. A thing, however, does not act solely in accordance with its archetypal or primarily intelligible being but also as it is subject to particular material conditions and possesses a particular individuality. Nothing therefore prevents our diverting the term *nature* from its primary significance to denote secondarily *what a thing is as* individual ". It is easy to see how the mistake could be made of substituting for individual (which is of course meant technically in this quotation) such an entity as one particular species, variety etc., whereupon nature would be treated as well-nigh synonymous with essence. In any case, to understand the nature of a thing is to go far towards determining its essence, which is the first desideratum of Logical Division. That Linnaeus did not confine himself strictly to the philosophical definitions in his use of the idea of the individual is already apparent from his comparison of it with the *species infima* quoted above (p. 150). It is likely that for him a " natural " system was one that showed the *natures* of things, and that natures meant in practice essences.

It is true that Collingwood (1945), for example, considers a great revolution in the idea of Nature (in general) to have begun with Copernicus (1473–1543) and Bruno (1548–1600) and to have gone far by the eighteenth century, in fact to have begun by then to be superseded by the modern outlook, the first signs of which are found in Turgot's *Discours sur l'histoire universelle*, 1750, and Voltaire's *Le Siècle de Louis XIV*, 1751. Linnaeus, however, was still content to use the doctrine of the construction of the flower which was advocated by Cesalpino in the sixteenth century. In this, as Sachs has pointed out (1906, p. 104) empirical findings might have caused him to change his attitude ; but there was nothing to disturb his ideas on the principles of classification that classified things, so reasonably, by their essences and (by a slight extension) their natures. To that extent he was indeed using a natural classification, expressing the principles on which the existence of this subjects depended—in short, in intention at least a taxonomy of analysed entities such as we would like to-day. Sachs's idea of a natural system as against an artificial one, however, appears to be one based on overall affinity. The two are by no means the same ; and, in fact, it is likely that Sachs, in reading Linnaeus, substituted his own for Linnaeus's meaning of "'natural " and in consequence praised him for being least Aristotelian exactly where he was being most so in intention. Linnaeus's insistence that all characters (in the modern sense) of the fructification should be taken into consideration sounds very like the modern empirical attitude ; but his restriction *on principle* of usable characters to those of the fructification (and his insistence that the habitus could never be used to the neglect of the fructification, *Phil. Bot.*, p. 209) shows the resemblance of his principles to those of Cesalpino. Nevertheless, his statement

(*Classes Plantarum*, 1747, preface) that into a natural Class can be admitted only those plants that are related (*affines*) to each other and agree in their *whole aspect* (*Facies*) and nature suggests that he might at times relax a little from confinement to the fructification. The theoretical basis of his procedure is made perfectly clear and explicit by Ray (1703) who begins his essay "De Methodo Plantarum in genere" with the words *Definitio perfecta conficitur è Genere proximo et Differentia essentiali: At essentiae rerum nobis incognitae sunt, proinde et Differentiae earum essentiales. Verum cum ex eadem essentiâ eaedem qualitates, operationes, aliaque accidentia fluant, non alia certior convenientiae essentialis seu genericae nota esse potest, quàm plura habere attributa communia, seu plures partes et accidentia similia, vel totam faciem, habitum, et texturam eandem.* "A complete Definition is made up out of a Genus proximum and an essential Difference: but the essences of things are unknown to us, and therefore the essential Differences of them also. However, since from the same essences flow the same qualities, operations, and other things which are accidents, there can be no surer mark of essential, and so of generic, agreement than to have many common attributes, that is, many parts and accidents similar, or to have the whole facies, habit, and structure the same." This passage shows that Ray was clearly aware of the difficulty of constructing a taxonomy of analysed entities for plants (and of course equally for animals) by the use of Logical Division and proposed to overcome it by using overall affinity as a clue to essential similarity or difference. Linnaeus did the same, but since the fructification must be of the first importance on purely Aristotelian principles, he had to confine himself in the first place to overall affinity as shown by it.

Memory.

(i) *Requirement and Consequences.*

Linnaeus states explicitly and repeatedly that the botanist (and, since his rules apply equally to all kingdoms of Nature (*Crit. Bot.*, preface), the zoologist too) must know all genera, and commit their names to memory (e.g. *Crit. Bot.*, aphorism 213, 218, 251; *Phil. Bot.*, 256) but cannot be expected to remember all specific names (*Crit. Bot.*, 213; *Phil. Bot.*, 256). I think the practical reason for this requirement is fairly evident. Species in the aggregate were too numerous to be remembered and in detail often hard to determine and define clearly. The largest groups often varied greatly in the works of different botanists who had based their systems on different attributes, e.g. on the shape of the leaf (de l'Obel) the corolla (Rivinus) the calyx (Magnol) or, as far as was then possible, on general affinity (Ray). Consequently there was the greatest difficulty in comparing the system of one botanist with that of another, since the constituent groups would differ in name and contents and the identification of the same species in different systems would not always be easy, especially since the same species would acquire different differentiae as it was moved from genus to genus. However, there was some hope of general agreement on genera, which, if they could be defined clearly and given distinct names, could be treated as the practical units of classification. Whatever system was employed, the genera could stay the same (*Crit. Bot.*, 216) and be arranged in larger groups according to what particular criteria were chosen. Then neither the names of the genera would be changed according to the system used (*Crit. Bot.*, 216) nor would their definitions (*Phil. Bot.*, 202), and the concept of each genus would not become confused and indistinct in the mind (*Crit. Bot.*, 216, 224, 225), all of which things Linnaeus explicitly said were to be avoided. Consequently, there would be far less burden on the memory, and far greater stability in nomenclature. The genera and their names being fixed, comparison of the literature would be simplified without either pinning the botanist down

to one system of classification or requiring a firm decision on every species before any comparison could be made. Moreover, as Joseph (1916, p. 87) remarks, the genus is often presented to us (after we have become acquainted with some individuals) before it can be defined. " . . . the use of general names shows that some apprehension of their common nature comes to us from the beginning along with an experience of individuals; only we may long remain unable or not endeavour, to formulate it." The genus, therefore, is to that extent a suitable entity to expect agreement on.

As consequences it followed that genera must be, as Linnaeus said,

(i) " natural " (so that there would be general agreement on them);
(ii) the smallest groups above species;
(iii) distinct (so that every species would fall clearly into place in one or other, with no untidy intermediates and unplaced forms. This is a requirement also of Logical Division).

Moreover, every generic name, to be efficient as a mnemonic should be

(i) univerbal (to be as concise as possible);
(ii) distinct, not compounded out of other generic names nor modifications of them (which would suggest indistinct and intermediate groups);
(iii) literally meaningful, not meaningless and therefore hard to retain in the memory;
(iv) expressing (if possible, but Linnaeus recognized how seldom this rule could be obeyed) the peculiar characteristic of each genus, so that the name would also be a diagnosis: or at all events,
(v) not contradicted by the features of any species within the genus (or people would think, on arriving at it, that they had made a mistake in identification).

It was not long before the weight of empirical evidence made it impossible to maintain most of these rules; at present, the use of one word only for a generic name is still in force, and for the same reason, but the rest have gone. It is interesting to note one other survival. As the generic name was a single word referring to a kind of thing, and therefore requiring a definition, but the specific name was a phrase acting as a differentia, Linnaeus was quite right in forbidding tautologous names. Such a name as *Troglodytes troglodytes* was not a name at all to him (or only a trivial name) since it was a mere repetition of the generic name with no differentia; under no conceivable circumstances whatever could the name of a genus be also the differentia of one of its species. His (rational) dislike of tautologies is still to be met with in botanical nomenclature, where, however, it is applied to the trivial name in which it does not matter in the least and I find in conversation that this taxonomic Malapropism is justified on " aesthetic " grounds.

(ii) *Natural Genera.*

Linnaeus expressed his opinion on the " naturalness " of genera with considerable emphasis. " Genera, on the other hand [in contrast to species] are as many as there are, of distinct species, common proximal attributes [i.e. nearest in the ranks of Logical Division to the attributes of particular species] according to which they were created in the beginning: this is confirmed by revelation, discovery, observation. Hence *All Genera are natural* . . . And so we must by attentive and careful observation inquire into the limits of Genera, since *a priori* they are determined with greater difficulty, although this is the task which must be undertaken for *the confusion of genera brings inevitably the confusion of everything* (Caesalpinus) . . . And so I urge all on sensible

Botanists as a thing to be recognized if any certainty in the art is to be desired, that all *Genera and Species are natural*, without the adoption of which principle no soundness in the art can be achieved." (*Genera Plantarum*, pp. II, IV-V.)

I suggest that this principle which must be adopted (*assumto*) is in reality an assumption in the modern sense, which is made desirable by the sound practical reasons given above, and that revelation is brought in to confirm it, as something of a rationalization. He repeated many times the statement (quoted from Cesalpino) that if genera are confused all is confused (e.g. *Genera Plantarum*, introduction ; *Crit. Bot.*, 225 ; *Phil. Bot.*, 159). Even a glance at the works of some of his predecessors is enough to show the difficulties he and they must have had when comparing the systems, groups and definitions of different authors, and to evoke the liveliest sympathy for his earnest desire to do something practical about it. Nevertheless the problem was primarily a practical one and his solution can hardly be said to be confirmed by revelation. It may well have been by experience.

(iii) *Monotypic Genera.*

From the quotation given just above, it appears that for Linnaeus each genus differs in (at least) one particular attribute from its nearest relatives (in accordance with Logical Division) and must be the smallest group of species. Genera, in fact, are the Genera proxima of Logical Division. This must not be taken to mean that single species can be split off from a genus and made into separate genera on the basis of their *specific* characteristics ; we must not agree with those " who think that they can divide a genus with the best of reasons in whatever way they like when they have discovered the smallest characteristic, the cause of their false report ". (*Crit. Bot.*, 215). His exact words for the last phrase are " *dum minimam investigarunt notam falsi testimonii caussa*". Such a *nota* (character in the modern sense) might of course be characteristic only of that particular species. He fully agreed that there are indeed genera containing only a single species each (*Phil. Bot.*, 203). As a consequence, since the specific name was a differentia, he maintained with perfect consistency that a species which is the only one in its genus cannot have a specific name (e.g. *Genera Plantarum*, Ratio Operis, 4). How can one possibly know whether another species will be discovered, and when it is what its characteristics will be ? But no true differentia can be given to either, until these are known (*Crit. Bot.*, 293).

How then can one distinguish between a merely specific attribute and one which, although carried so far as is known only by one species is nevertheless sufficient to require a generic distinction ? Unless some criterion can be found there can be no certainty. This is a difficult question and it is not surprising that Linnaeus's views on it are not too clearly stated. One possible solution would be to take one particular structure *a priori* and make the variations in it of generic importance, in the same way as within his artificial system the Classes are taken from the stamens and the Orders from the position of the ovary. Difference in fructification is his criterion for the foundation (*fundamentum*) of genera (*Phil. Bot.*, 98). But even then, he says that since there are variations in some parts of the fructification at least, in most genera, it would be easy to arrive at a state in which there were as many genera as species (*Phil. Bot.*, 170, 175). Some more modern systematists (e.g. G. M. Mathews in his *Birds of Australia*) have well-nigh reached this state. Linnaeus's own words are merely (*Phil. Bot.*, 159) that " We say there are as many genera as there are similarly constructed fructifications revealed by diverse natural species" . Ortega (1792), as Svenson points out, had already realized and stated the consequences of this remark, namely, that, unless there are more species than one in a genus it is

not possible to know what are generic and what specific attributes, and that Linnaeus was on dangerous ground when asserting the existence of monotypic genera.

Linnaeus himself said that a definition of a genus (*character*) was not infallible until it had been checked on all the species (*Phil. Bot.*, 193), that the greater the number of species in which a particular character (*nota*) was found to be constant, the more likely it was to be of generic value (*Phil. Bot.*, 169), that the *habitus* could be used to check the "naturalness" of a genus (*Phil. Bot.*, 168) but never in place of or to the neglect of the fructification (*Phil. Bot.*, 209), that although variation occurred in the fructification in most genera all the parts did not vary at once (*Phil. Bot.*, 170) and that if the flowers agree, a species should not be split off from the genus on differences in the fruit (*Phil. Bot.*, 177). All this suggests strongly that he was in fact recognizing "natural" groups, as far as possible, by means of the character-complex (Cain, 1953, p. 25; 1954), in which the importance of characters is determined by their covariation with all other characters in the complex. Then no single character within the complex is of magistral importance, and characters otherwise present throughout may be absent in one or other species, which is not separated from the genus on that account because all the other characters in the complex clearly tie it to that genus. This is a feature of a natural classification in the modern sense, and it is not surprising, therefore, that his practice should be so similar to the modern (although his principles were so different, p. 154) as to mislead the far from uncritical Sachs over his ideas of the natural classification.

This interpretation is confirmed by a letter of the younger Linnaeus, my knowledge and the following translation of which I owe to the kindness of Dr. Arvid H. Uggla of Uppsala. The letter, dated 21 April 1778, is to Dr. Abraham Baeck, who was preparing his oration in memory of Linnaeus, to be given before the Academy of Science in Stockholm, and had asked certain questions about the elder Linnaeus's ideas. The passage in question is as follows. Latin words in parenthesis stand so in the letter instead of Swedish words.

"My Father's secret art of determining (delimiting) genera in such a way that Species should not become genera? This was no other than his practice in knowing a plant from its external appearance (externa facie). Therefore he often deviated from his own principles in such a way that variation as to the number of parts (numero partium) did not disturb him, if only the character of the genus (character generis) could be preserved. Foreigners don't do so, but as soon as a plant has a different splitting (cleavage) of the corolla and calyx, or if the number of stamens and pistils (numerus staminum et pistillorum) varies, they make a new genus. This is what Aublet, Forster and others have done. If possible he (Linnaeus) tried to build the character genericus on the cleavage of the fruit so that all species that constitute a genus should have the same shape of their fruit.

"I have accepted the same principle in my *Mantissa*. In this way some among Forster's genera will have to suffer, which I have told him. Maybe this will not please him, which might explain why for some time I have had no letters from him."

As a result of this procedure Linnaeus had arrived at or retained a large number of natural groups, many of which were clearly marked off from each other, and each of which was a close-knit group of several species. When he came across a species that was as distinct from these groups as they were from each other, it would seem that he placed it in a separate genus to mark the degree of its difference, by a simple extension of his method for avoiding the complete fragmentation of genera. This, as mentioned above, is the modern procedure in which the taxonomic hierarchy above the species is used as a rough indication

of the homogeneity of the groups (and so of the gaps between subgroups) but it is a departure from strict Logical Division.

Here again is an instance of the conflict in the Linnaean system between his adherence to the principles of Logical Division—because they were in so many ways so reasonable, so much common sense—and his constant attempts to recognize natural groupings on overall affinity. Another example is his insistence that some characters (colour, size, taste, etc.) are never of specific value. Granted that they are often demonstrably variable within many if not most species, it does not follow that any of them are always utterly worthless, nor in fact did he so treat them always in practice. But obviously in Logical Division each species must be marked off by some essential difference and this clearly cannot vary within the species. Consequently he was bound to reject in theory all characters known to vary conspicuously, and bound to overlook the fact that if one defines species as "breeding true" and demands also that each species shall have its characteristic difference, one may be led into difficulties. Sibling species are precisely those which have only trivial morphological differences but do not interbreed to any extent in the wild, and are, biologically speaking, good species. Linnaeus's own principles inevitably blinded him to the possibility that such should exist, and indeed it remained unrecognized for a long time afterwards.

(iv) *Distinctness of Genera.*

That taxonomic genera should be distinct follows immediately from the use made by Linnaeus of Logical Division, in which they are merely one example of genera subalterna. The requirement was, however, strongly reinforced in practice by the necessity of memorizing them. Many times he says that we must have distinct names, distinct genera, distinct concepts, or all will be confusion. The limits of genera will only be known, he says, when all the species are discovered, and similarly those of classes when all the genera are known (*Phil. Bot.*, 160). This is obvious for the system based on overall affinity, but he does not restrict the application of the last remark explicitly to natural classes. However, as artificial classes are stated to be only succedanea for natural ones (*Phil. Bot.*, 160; *Genera Plantarum*, p. 6) the application seems reasonable. When all species are known, it will then be evident what characteristics are only specific or common to a few species within a natural genus, and what are truly generic.

But this implies either (*a*) that there are diagnostic characters of all genera, or (*b*) that there are not, but it will always be found that natural groups (recognized by their character-complexes, not by single diagnostic characters) are separated by clear gaps from their nearest relatives. The second implication, as already mentioned, probably did not occur to Linnaeus, and he would have subscribed to the first. But in the present evolutionary taxonomy, it is possible that distinct genera will be found to change imperceptibly as one passes backwards in time, with no obvious breaks or gaps until they merge into one another. It is also perfectly possible that between two close-knit clusters of species at the present day there should be not a clear gap but one sprinkled with species intermediate in character. In fact the situation is not uncommon. Since there is no law quantifying the angles of divergence of phyletic lines (Cain, 1956) and very good reason to suppose that none will be discovered, the Linnaean insistence on the distinctness of genera cannot possibly be maintained. The genus is, in fact, a much more dubious entity than the species. But we still follow the practice, which derives entirely from Logical Division, of insisting that every species must be included in one and only one genus. No provision for recognizing intermediates is made.

Bases of the Linnaean System.

As a result of even this brief and incomplete survey of the principal features of Linnaeus's taxonomy it can be seen that much of it is attributable to three things, namely, the principles of Logical Division, the insistence that all genera must be memorised, and of course the actual empirical evidence obtained from the study of plants, which was sometimes in serious conflict with the requirements of the other two. The feeling for overall affinity and presumably the hope of attaining to a system which would reveal the natures of plants, drove him to work at his great desideratum, the natural system. He first, according to Sachs, saw clearly that no natural system could be based on *a priori* principles. As explained above (p. 155) I think this is incorrect or rather that if Linnaeus did come to that conclusion in practice, his practice was a little ahead of his own theory. Even in genera, where he was expressly concerned with the establishing of natural groups, he insisted (with some slight modifications, perhaps, in practice) that the generic distinctions must be based on the fructification, for reasons which were purely Aristotelian in theory. In a truly empirical system there is no such must ; no one part can be pointed to as *a priori* more important than any other. If in fact genera are still defined on the fructification, it must be either because, as suggested above, that provides the largest character-complex in the plant, and so is likely to be the best basis for an estimate of overall affinity, or perhaps, in some groups, because of strong conservatism.

It is clear that in its theoretical basis, the evolutionary taxonomy of the present day shares with Linnaeus's taxonomy only the binominal nomenclature as a reference system (which is now often an embarrassment since it places so much emphasis on genera) and the names Class, Order, Genus, Species and Variety as rank-names in the hierarchy, and perhaps the concept of the species as "breeding true", which is applicable only to bisexual forms. Whatever else it shares is likely to be a remnant from the principles of Logical Division, retained only because they can still be made to apply to badly-known groups and because taxonomists in general are too overworked to have time to study the theory of taxonomy. It is more than doubtful whether we should call the present system of taxonomy Linnaean at all.

If we are to have a truly scientific taxonomy, we must first ask whether classification *per genus et differentiam* is applicable to evolutionary continua at all and, if so, whether in itself it causes any bias in the presentation of the data. We must also ask whether the binominal nomenclature, which is a direct product of this mode of classification is so firmly established in the literature as to make a fundamental reform impossible although desirable.

But, more important still, we must ask how far the principles of Logical Division, whether explicitly recognized as such or not, are still in use in present-day taxonomy, especially in those groups with little or no known fossil history. It is frequently said—indeed I have said it myself (Cain 1953. p. 18)—that when the theory of descent with modification was established all that taxonomists had to do was to equate close affinity with descent from a proximate common ancestor, less close affinity with descent from a more distant one and carry on as before. Consequently Darwin could take the classification as produced by non-evolutionary taxonomists and point out the complete concordance between it and the consequences of evolutionary theory. This was no doubt true for well-known groups in which overall affinities had been carefully worked out (and nowadays for groups in which the fossil history is very completely known). But in groups with little or no fossil history especially in those with very large numbers of closely related forms whose affinities seem to make up a veritable reticulum the classification adopted may often depend

very much on just what characters are regarded of primary taxonomic importance i.e. what is taken as *fundamentum divisionis* for the first division ; indeed a change of emphasis from one class of characters to another may involve a complete reclassification of the group. In such circumstances, it is essential that the taxonomist should rid his mind of all preconceived notions of what " must " be more primitive, or more important in any other theoretical way, and adopt the purely empirical approach, beginning with species or taxa at and around this rank, and grouping them into higher and higher natural groups using all possible classes of evidence. There is no " must " for any particular sort of character whatever (p. 161). The result will be not only a salutary exercise in intellectual humility for the taxonomist concerned, but an arrangement free from individual quirks of theory, and therefore the most useful and stable.

Summary.

1. The principles on which Linnaeus based his taxonomy are shown to be, at least in intention, primarily Aristotelian.

2. He, like others, was trying to produce a classification founded on the real natures of organisms, not on superficial resemblance ; the method he adopted was to classify by the rules of Logical Division, which involve the determination of the essence of each entity.

3. Consequently his idea of a natural system was not that in use at the present ; certain comments by historians of science are therefore incorrect.

4. A distinction is made between taxonomies of analysed and of unanalysed entities. Logical Division is appropriate only to the former.

5. Linnaeus's classificatory unit was the genus, not the species. His principles led him to assert that all genera must be distinct and natural ; moreover, since they were stable units, however much the higher groups of a classification changed from author to author, he insisted that their names must be memorized.

6. Most of his rules of nomenclature follow directly from this requirement that the botanist must know and remember all genera.

7. The increase in knowledge of plants since Cesalpino had already led to the breakdown of at least one important theoretical grouping ; in Linnaeus, the conflict between theoretical requirements and actual facts is very evident. Because of it, his practice often approached the modern when his theory did not.

8. It is suggested that the principles of Logical Division, unrecognized as such, may still be a powerful source of unwarranted bias in modern classifications.

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GENETIC STABILITY IN THE SNAIL CEPAEA NEMORALIS [L.] : A FURTHER EXAMPLE

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(With 1 text-figure.)

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In a previous paper (Goodhart, 1956) a comparison was made between some samples of the polymorphic land-snail *Cepaea nemoralis* (L.) collected by the late Mr. H. H. Brindley in 1906 and 1911 from small carefully defined areas, and further samples from the same localities taken in 1953. In some of the colonies the percentages of different shell colour and banding pattern morphs had remained remarkably constant over the 40-year period between the samples. On p. 58 of that paper a further collection, made by Mr. Brindley in 1892, was mentioned but its exact locality had not been identified. A reference has now been found (Brindley, 1904) which does make this clear, and further samples were collected from the area in 1956. Once again there is evidence of considerable genetical stability and there are other features of interest, as well as the long period covered by the observations, that may be worth recording.

The relevant passages from Brindley's article, on p. 122 of the *Local Natura-*

History Guide for the Cambridge Meeting of the British Association for the Advancement of Science in 1904, are as follows :—

> " During the Long Vacation of 1892 on a day when the river was in flood the writer found the raised foot-path across the meadows from Waterbeach Station to Bottisham Lock crowded with individuals of these two species, which had found refuge thereon from the water covering the grassland on either side. Of 639 specimens of *Helicogona arbustorum* picked up haphazard from 80 yards of the footpath . . . Of 261 adult examples of *Helix nemoralis* taken from the same spot 21 were without bands, and were mostly brownish in colour, a few being orange or yellow. The banded specimens forming the majority were of most of the usual colours, while the banding varied so greatly as to defy any summary expression, as is so often the case in this species."

It seems plain that this refers to the footpath which runs for about 100 yards along the top of an old flood bank from Waterbeach Station across the fen towards the River Cam, the Ordnance Survey map reference being 502650. The glass-topped case, in which the collection is preserved in the University Museum of Zoology at Cambridge, has with it labels saying that the shells were collected " within an area of 80 square yards in a meadow near the Cam ", at Waterbeach in August 1892, and that 237 are banded and 24 not banded, making a total of 261. Actually the case contained 276 shells when they were counted in 1956, of which about 15 were small first-year specimens, four of them fragmentary and unclassifiable. The remaining 272 shells have been re-examined and classified for colour and banding patterns, according to the usual system as described in the previous paper, and are shown in Table I.

TABLE I.—Analysis of *Cepaea nemoralis* samples from Waterbeach. All the 5-banded fusion patterns are aggregated as " 12345 fused ", and 4-banded as " 02345 fused ", but the different formulae are shown separately in fig. 1. All the brown shells were unbanded, and the number of yellow shells will be the total for each sample, less the brown and pinks.

	1892 Living	1956, Living			1955–56 Dead
		May	Sept.	Oct.	
12345	105	54	17	33	44
,, fused	47	43	14	21	26
02345	21	23	9	9	18
,, fused	2	5	9	3	2
02340			1		
10345	28	3	1	2	10
12045	1				
Effectively banded	204	128	51	68	100
00345	31	23	3	9	20
003(45)		3		2	1
00340	8	22	1		4
00300	3	3	2	6	4
00045	2				
00000	14	5			2
Brown	10	3	3	7	4
Total	272	187	60	92	135
Pink	47	78	22	34	57
Dotted	98	85	34	31	45
Smudged	32	12	6	2	2

Three further samples of living snails were collected from this bank on 29 May, 22 September and 1 October 1956, and they are shown separately in Table I. They do not differ significantly from each other so, in fig. 1, they have been aggregated together and are treated as a single homogeneous sample of 339 snails. The 10 per cent more " effectively banded " shells in the two autumn collections, compared with the May sample, is well short of statistical significance.

Fig. 1 shows that the 1956 population is essentially of the same type as that of 1892. In this very variable species different colonies, even close together in quite similar environments, often show much wider differences in the various varieties present, and so it does seem that there is real evidence of continuity in the colony at Waterbeach. The general problem of variation in *Cepaea nemoralis*, with references to other work on the subject, has been discussed fully in the previous paper.

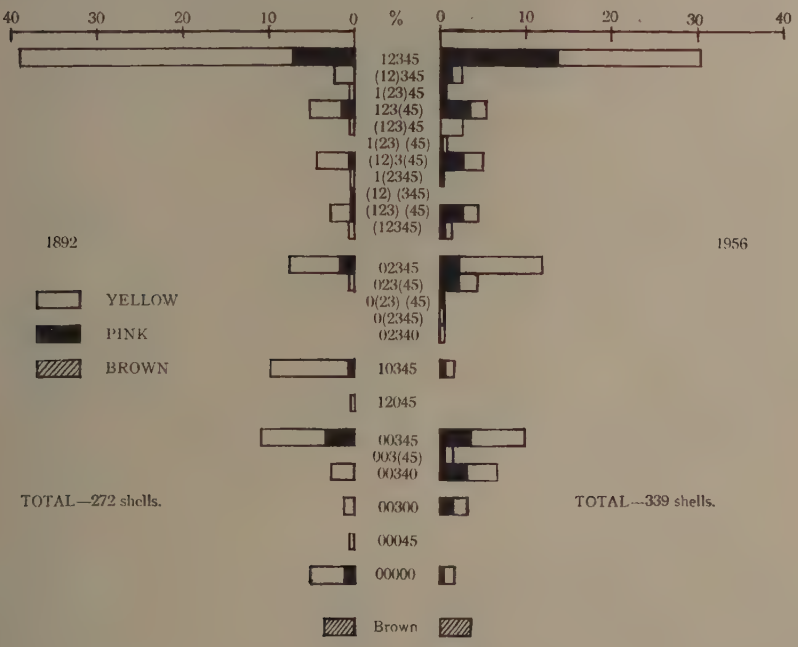

FIG. 1.—Composition of the *C. nemoralis* populations at Waterbeach in 1892 and 1956.

It is interesting to see that there had been practically no change at all, from 75 per cent in 1892 to 73 per cent in 1956, in the percentage of " effectively banded " shells, with one or both of the two uppermost bands present, as defined by Cain & Sheppard, 1950. The proportion of shells with all five bands present, fused or unfused, also shows little change from 56 per cent in 1892 to 54 per cent in 1956. There were 9 per cent more shells with all five bands present and unfused, formula 12345, in 1892 compared with 1956 and, although this is not statistically significant, it is likely that there was some real increase in total band fusion for all formulae, over the period.

There have, however, been some changes in individual banding formulae which are significant. The most obvious is for the 10345 formula, a well-defined pattern with the second band missing. In 1892 this was the third

most common formula comprising 10 per cent of the total, but in 1956 it was reduced to 1·8 per cent, while the 02345 formula, with the first band missing, increased from 8·5 per cent to 17 per cent. Both of these differences are significant at the 1 per cent level. Pink and yellow unbanded shells, formula 00000, a pattern due to a gene dominant to all others, are unusually rare in both samples and have decreased from 5·1 per cent to 1·5 per cent over the sixty years, the difference being significant at the 2 per cent level. Unbanded brown shells remain steady but uncommon at 3·7 per cent and 3·8 per cent.

The most obvious difference to be seen in fig. 1 is in the proportion of pink shells, the pink colour being genetically dominant to yellow, which appear to have increased from 17 per cent to 40 per cent. Unfortunately, however, the 1892 collection has been exposed to the light for 60 years and all the pink shells show serious fading, and so are difficult to classify for colour, nor are there any contemporary records for the colours as there are for the banding patterns. As the collection now stands, even if all the shells about which there is any doubt at all are classified as pink, it cannot be denied that there is a substantial and significant difference between the samples ; but after so long a period it is impossible to be certain that some shells may not have lost all traces of their original colours. Consequently it cannot be claimed confidently that there has really been a colour change in the colony, although that does seem likely.

There has been a change in the proportion of shells with fused bands (shown by brackets in the formulae), which are genetically dominant to unfused bands, and fused bands have increased from 18 per cent to 29 per cent of the total, a difference which is significant at the 1 per cent level. Finally, in Table I is shown the percentage of shells with dotted bands (var. *punctata*) due to a recessive gene, which has increased significantly from 36 per cent to 44 per cent in 1956, and also of shells in which the bands appear to be smudged. This smudging effect, which is not easy to classify, is found in 12 per cent of the 1892 sample but in only 5·9 per cent of the shells collected in 1956. The probability of this is less than 0·02, and the difference is perhaps greater than it seems from the figures, since in 1892 the smudging effect was more marked than in 1956, and many of the shells were so smudged that they were hard to classify for banding patterns. The smudging can hardly have been accentuated by fading, but it is not known definitely to be genetical in origin.

As well as the living snails collected in 1956 two samples of empty shells predated by birds and rats were collected from the same area, on 10 December 1955 and 4 March 1956. These two collections were not significantly different, so they have been aggregated as a single sample of 135 dead shells shown in the last column of Table I. There is no evidence at all of any differential selection for shell colour or pattern in these predated shells ; 74 per cent are "effectively banded" compared with 73 per cent in the living snails, 42 per cent compared with 40 per cent pink, and both have 4 per cent brown shells and 29 per cent fused bands. It is curious to see, however, that the predated sample does have significantly more of the 10345 formula, which forms 7·4 per cent of the total compared with 1·8 per cent of the living snails.

Discussion.

The *Cepaea nemoralis* colony along the bank at Waterbeach in 1956 was clearly essentially similar genetically to the colony occupying the same area in 1892, and there is every reason to believe that the present population has direct continuity with the one sampled by Brindley 64 years earlier. Mr. W. E. Doran, Chief Engineer of the Great Ouse River Board, has very kindly looked up his records for this area and is of the opinion that the bank was almost

certainly in existence in 1833, the date of an early map of the Survey of the Bedford Level, and he can find no record of any substantial changes having been made to it since long before 1892. The snail colony is therefore unlikely to have been seriously disturbed since the time of Brindley's observations, and the occasional floods certainly never reach to the top half of the bank to drown all the snails.

The situation is comparable with the one discussed in the previous paper, where two samples had been taken at an interval of 42 years from Cracknow Hill Plantation, a wood near Cambridge, and showed few signs of any significant changes having occurred over that period. The Waterbeach collections are interesting, however, not only in covering a longer period of time, but because they are both from the same very small and well-defined area of about 80 yards by 10 yards, instead of from a 25-acre wood. The two samples really are, therefore, strictly comparable and the numbers are large enough for some of the rather small changes that have occurred to be assessed statistically for significance.

The constancy of the " effectively banded " patterns is noteworthy, though it is a pity that there must be doubt about whether or not there has really been any change in shell colour. Both the shell colour and banding patterns are thought (Cain & Sheppard, 1954) to be controlled at least partly by selection by visual predators, but here it looks as though the population is in equilibrium and there is little evidence of differential predation at the present time. The only significant changes are in certain individual banding formulae, and also in the dotting and smudging effect, and these are less likely to influence predator selection, though they could be associated with other factors of selective importance. There are some small changes in the population to be seen after 60 years, which is perhaps to be expected, but whether they are the result of random fluctuations in gene frequencies, or of genetical selection, cannot be determined. The effect is, anyway, rather a small one.

The conclusion to be drawn from this Waterbeach colony together with the other cases described in the previous paper must be that, although there is wide genotypical variation between different populations of *Cepaea nemoralis* in different areas, the individual colonies not infrequently show a considerable degree of genetical stability in time.

Summary.

Samples of the polymorphic snail *Cepaea nemoralis* were taken from a colony covering a small area, with an interval of 64 years between the collections. There have been some small, but statistically significant, changes in the relative abundance of certain shell varieties over that period, but the general picture is of a population showing a high degree of genetical stability. There is no evidence of differential predation by birds or rats.

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